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FUNGUS FAIRY RINGS IN EASTERN COLORADO AND THEIR EFFECT ON VEGETATION

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INTRODUCTION

The present paper deals with fairy rings caused by fleshy fungi. The rings due to other causes, such as the grass rings, are not considered. The fungus rings are marked either by the fruiting bodies of the fungus or by a stimulated or a depressed growth of the natural vegetation or the cultivated crop. Fairy rings may become so abundant locally as to affect materially the crop yields of fields. On lawns they cause unsightly bare spots and dark-green areas, and in small experimental plots cause either a total loss of crop or a greatly increased yield. They are undesirable in all cases, and their eradication is a matter of practical importance. The studies herein recorded were made on the High Plains at Akron, Colo., during the period 1907 to 1916, inclusive. The soil studies were made during the summers of 1914, 1915, and 1916. The native vegetation at Akron has already been described in some detail (Shantz, 1911).[1] It is typical short grass, composed largely of *Bouteloua gracilis* (*oligostachya*) and *Bulbilis dactyloides*.

The term "fairy ring," generally used to describe the arrangement of plants in an approximately circular form, originated in the belief that these circular growths marked the paths of dancing fairies. Early literature is filled with tales of superstition concerning these rings. The superstitions varied somewhat with the different countries. In Holland these circles often marked the places where the devil churned his butter. The presence of such a ring on a farm caused an inferior quality of butter if the cows ate the grass from a fairy ring. In France many people could not be induced to enter one of these rings, because enormous toads with bulging eyes abounded there; but no harm was experienced if the rings were unintentionally entered at night. In Sweden a person entering a fairy ring passed entirely under the control of the fairies. Treasures were marked by such rings in many places, but these riches could not be secured without the help of fairies or witches. In England it was regarded

[1] Bibliographic citations in parentheses refer to "Literature cited," p. 242-245.

as a good omen to build a house on land showing these circles. In German mythology it was said tracks were traced in the dew the next morning after the fairies had danced. The circular spots where the grass had dried up were places where a glowing dragon had rested after his nightly wanderings.

The earlier natural causes assigned to these rings were almost as fantastic as the supernatural. Thunder, lightning, whirlwinds, ants, moles, haystacks, urine of animals, etc., were at different times supposed to be the cause of these rings. The following are some of the more common names applied to these circles; and usually indicate the supposed cause of the ring:

ENGLISH	FRENCH	GERMAN
Fairy rings.	Anneaux magiques.	Elfenringe.
Fairy circles.	Cercles magiques.	Hexenringe.
Fairy green.	Cercles du sabbath.	Hexenplatz.
	Cercles des fées.	Hexentanzplatz.
DUTCH	Cercles mycéliens.	Hexenkreise.
Heksenkringe.	Cercles mycogènes.	Hexentanze.
Kolringe.	Cercles de sorcières.	Zauberringe.
Tooverkringe.	Danses de fées.	Pilzringe.
Duivels Karnpad.	Ronds de fées.	SWEDISH
Duivelstjeinpad.	Ronds de sorcière.	
Tjenmolenpad.		Elfdans.

CAUSE OF FAIRY RINGS

As indicated in the introduction, the cause of the fairy rings was obscure for a long time. At first these rings were ascribed entirely to supernatural influence. Later they were attributed to various natural causes.

Bradley (1717, pt. 3, p. 122–123) gave two probable causes for fairy rings:

> (1) Just under the turf where the mushrooms were growing, was a tract or path made by pismires, which was not only hollow in many places at that time, but the very covering of that passage was made of earth extremely fine which those creatures had flung up: The fineness of the earth wrought by those laborious animals might very reasonably contribute to the extraordinary vegetation of the grass growing upon it, and the hollowness of the ground underneath might produce that moldiness within it which afterwards might be formed into mushrooms.
>
> (2) Garden-snails . . . , when they couple, always make choice of short grass to creep upon . . . leaving upon the grass where they crept, a viscous shining matter. So that it may be, that slime when it putrifies may produce the mushrooms we find growing in circles upon Commons.

It is interesting to note in connection with Bradley's observations that ants have often been found working in the marasmius fairy rings at Washington, D. C. They are probably attracted by the presence of the fungus.

Hutton (1790, p. 8), who published the results of observations on fairy rings extending over the period from 1776 to 1778, summarized the knowledge of the cause of these rings as follows:

I know that similar circles have been observed by naturalists, and by them ascribed to thunder; as we should certainly have done in this case, were it not for the regular annual progression, which, if the effect of thunder, must follow rules not yet investigated, either in electricity, vegetation, or the mineral system.

He examined the soil and found no clue. At times he also noticed the presence of fungi in the ring, but did not consider them significant.

Withering (1796, p. 222) definitely assigned the cause of fairy rings to *Agaricus oceades*.

I am satisfied that the bare and brown, or highly cloathed and verdant circles, in pasture fields, called *Fairy Rings*, are caused by the growth of this Agaric. . . . Where the ring is brown and almost bare, upon digging up the soil to the depth of about 2 inches, the spawn of the Fungus will be found, of a greyish white colour, but where the grass has again grown green and rank, I never found any of the spawn existing.

FUNGI CAUSING FAIRY RINGS

The tendency of all fungi to grow outward from the point of germination of the spore results in circular colonies in a widely varying group of fungi. Rings are often noted among the molds. This paper deals only with rings formed by Basidiomycetes.

The first fairy rings noted which were definitely assigned to fungi were caused by *Agaricus oceades*. Following this report many different species were associated with fairy rings.

Eleven years later Wollaston (1807) extended Withering's observations and reported rings formed by *Agaricus campestris*, *A. terreus*, *A. procerus*, and *Lycoperdon bovista*. Most of the writers following Wollaston have substantiated his results with the exception of the following: Persoon (1819, p. 4–5) called attention to the singular distribution of mushrooms in fairy rings, but stated that the cause was not well known. Lees (1869) attributed the cause of these rings to the action of moles. The burrows of these animals were supposed to be marked by the dead area in the fairy ring. Buckman (1870) believed that the fungi appeared as the result of the stimulation and death of the vegetation, and were not therefore the primary cause, although the ring was often continued and extended by them; in fact, he thought that rings to which fungi had not become attached soon broke up and disappeared. Gillet (1874, p. 22) states that it is difficult to explain the cause of the grouping of some species of mushrooms in fairy rings. Although it is understood that most of the writers thought that one species of fungus alone was the cause of a particular fairy ring, only a few writers stated so definitely. Greville (1828, p. 323) said that he never detected more than one species of fungus in the same ring. This statement was also made by McAlpine (1898). Williams (1901, p. 207) stated that fairy rings

showed a similar disposition to encourage the more luxuriant growth of other species of fungi that occurred elsewhere in the surrounding field.

In eastern Colorado the fairy rings were never known to have more than one species in the fruiting zone, although a ring of *Calvatia cyathiformis* was seen in fruit that had smaller rings of *Agaricus campestris* also in fruit, in the inside (fig. 9).

In Table I in the middle column are listed those species mentioned in the literature cited in this paper. The names used at the present time are given in the first column. Some of the forms can not be definitely assigned to species now known, since the citations were not definite enough in the original articles. To this list is also added the species causing the rings described in this paper, and a few of the fungi causing rings in the vicinity of Washington, D. C., noted by Miss Vera K. Charles, Assistant Mycologist of the Bureau of Plant Industry.[1]

TABLE I.—*List of fungi reported as causes of fairy rings and the names of the investigators*

IDENTIFIED FUNGI

Species.	Name used by author.	Investigators.
Agaricus arvensis Schaeff...	*Agaricus arvensis*.........	Buckman (1870) Atkinson (1900).
Do....................	*Agaricus (Psalliota) arvensis.*	Lees (1869).
Do....................	*Psalliota arvensis* Sch.....	Ballion (1906).
Agaricus tabularis Peck.....	....	Shantz and Piemeisel.
Agaricus campestris L......	*Agaricus campestris*........	Wollaston (1807), Jorden (1862), Shantz and Piemeisel.
Do....................	*Psalliota campestris*.......	Van Tieghem (1884, p. 1044–1045), Ritzema Bos (1901), Massart (1910).
Agaricus sp................	*Agaricus* sp..............	Olivier (1891).
Amanita muscaria L.........	*Amanita muscaria*.........	Ludwig (1906).
Amanita phalloides Fr......	*Amanita phalloides*.......	Do.
Boletopsis cavipes (Opat.) Henn.	*Boletus cavipes*...........	Do.
Boletus bovinus L..........	*Boletus bovinus*...........	Ballion (1906).
Boletus elegans Schum......	*Boletus elegans*...........	Ludwig (1906).
Boletus variegatus Swartz...	*Boletus variegatus*.........	Do.
Calvatia cyathiformis Bosc...	....	Shantz and Piemeisel.
Calvatia fragilis Vitt........	....	Do.
Calvatia polygonia Lloyd....	....	Do.
Cantharellus aurantiacus (Wulf.) Fr.	*Cantharellus aurantiacus*...	Ludwig (1906).
Cantharellus cibarius Fr.....	*Cantharellus cibarius*......	Lees (1869).
Cantharellus cinerus Fr.....	*Cantharellus cinereus*......	Ludwig (1906).
Catastoma subterraneum (Pk.) Morg.	....	Shantz and Piemeisel.
Clavaria sp...............	*Clavaria* sp..............	Münch (1914).
Clitocybe geotropa Fr.......	*Agaricus geotropus* Bull...	Lees (1869).
Do....................	*Agaricus (Clitocybe) geotropus* Bull.	Do.
Clitocybe gigantea Sow......	*Clitocybe gigantea*.........	Bayliss (1911).
Do....................	*Agaricus giganteus*........	Jorden (1862), Van Tieghem (1884), Ritzema Bos (1901).
Do....................	*Agaricus (Clitocybe) giganteus* Sow.	Lees (1869).
Clitocybe infundibuliformis Fr.	*Agaricus infundibuliformis* Sch.	Do.
Do....................	*Agaricus (Clitocybe) infundibuliformis* Sch.	Do.

[1] In the systematic portion of this work the writers are indebted to Mrs. Flora W. Patterson, mycologist in charge of pathological collections, for many suggestions; to Miss Charles for identification and additions to the list of fungi causing fairy rings; to Prof. W. G. Farlow, of Harvard University, for the identification of *Agaricus tabularis*, and to Prof. C. G. Lloyd, of Cincinnati, Ohio (see 1916), for the identification of *Calvatia polygonia*.

TABLE I.—*List of fungi reported as causes of fairy rings and the names of the investigators*—Continued

IDENTIFIED FUNGI—continued

Species	Name used by author	Investigators
Clitocybe maxima (Gärtn. and Meyer) Quel.	*Agaricus maximus* Gärtn. and Meyer).	Münch (1914).
Do	*Agaricus (Clitocybe) maximus.*	Do.
Clitocybe nebularis Batsch	*Clitocybe nebularis* Batsch	Stahl (1900).
Collybia confluens Fr	*Agaricus confluens* Pers	Lees (1869).
Do	*Agaricus (Collybia) confluens* Pers.	Do.
Collybia sp	*Collybia* sp	Münch (1914).
Cortinarius amethystinus (Sch.) Sacc.	*Inoloma traganum*	Ludwig (1906).
Cortinarius armillatus (Alb. and Schw.) Fr.	*Telamonia armillata*	Do.
Cortinarius traganus Fr	*Inoloma traganum*	Do.
Hebeloma crustuliniforme Fr	*Agaricus crustiliniformis* Bull.	Lees (1869).
Do	*Agaricus (Hebeloma) crustiliniformis* Bull.	Do.
Hydnum compactum Pers	*Hydnum compactum*	Ludwig (1906).
Hydnum repandum L	*Hydnum repandum* L	Lees (1869); Ballion (1906)
Hydnum suaveolens Scop	*Hydnum suaveolens* Scop	Thomas (1905); Coulter, Barnes, and Cowles (1911).
Hygrophorus virgineus (Wolf.) Fr.	*Hygrophorus virgineus* Fr.	Lees (1869).
Inocybe sp	*Inocybe* sp	Williams (1897).
Lactacius insulsus Fr	*Lactarius insulsus*	Ludwig (1906).
Lactarius piperatus (Scop.) Fr.	*Lactarius piperatus* Fr	Lees (1869).
Lactarius torminosus (Schaeff.) Fr.	*Lactarius torminosus*	Ludwig (1906).
Lepiota morgani Peck	*Lepiota morgani*	Williams (1901), Shantz and Piemeisel.
Lepiota procera (Scop.) Quel.	*Agaricus procerus*	Wollaston (1807).
Lycoperdon bovista L	*Lycoperdon bovista*	Do.
Lycoperdon gemmatum Batsch.	*Lycoperdon pratense* Pers	Ballion (1906).
Lycoperdon cyclicum McAlpine.	*Lycoperdon cyclicum*, n. sp.	McAlpine (1898).
Lycoperdon wrightii B and C.		Shantz and Piemeisel.
Marasmius oreades (Fr.) Bolt.	*Marasmius oreades*	Lawes, Gilbert and Warrington (1883); Williams (1897); Coville (1898); Massart (1910); Bayliss (1911).
Do	*Marasmius oreades* Fr	Molliard (1910).
Do	*Marasmius oreades* Bolt	Ballion (1906).
Do	*Agaricus orcades*	Withering (1796).
Do	*Agaricus caryophylleus* (Sch.) Schroet.	Reed (1910).
Do	*Agaricus oreades*	Wollaston (1807); Jorden (1862); Buckman (1870); Van Tieghem (1884); RitzemaBos(1901); Ludwig (1906);Lees (1869).
Marasmius urens Fr	*Marasmius urens* Fr	Lees (1869).
Morchella esculenta (L.) Pers.	*Morchella esculenta* Bull	Ballion (1906).
Morchella hybrida Pers	*Mitrophora semilibera* DC.	Do.

TABLE I.—*List of fungi reported as causes of fairy rings and names of the investigators*—continued

IDENTIFIED FUNGI—continued

Species.	Name used by author.	Investigators.
Paxillus involutus (Batsch.) Fr.	*Paxillus involutus*	Ludwig (1906).
Pluteus cervinus Schaeff.		Charles.
Tricholoma columbetta Fr.	*Tricholoma columbella*	Massart (1910).
Tricholoma equestre L.		Charles.
Tricholoma grammopodium Fr.	*Agaricus grammopodius* Bull.	Lees (1869).
Do	*Agaricus (Tricholoma) grammopodius* Bull.	Do.
Tricholoma melaleuca (Pers.) Quel.		Shantz and Piemeisel.
Tricholoma personatum (Fr.) Quel.	*Agaricus bicolor*	Münch (1914).
Do	*Agaricus personatus*	Buckman (1870).
Do	*Agaricus (Tricoloma) personatus* Fr.	Lees (1869).
Tricholoma praemagnum	*Tricholoma praemagnum*	Ramaley (1916).
Tricholoma sp.	*Tricholoma* sp.	Williams (1901).
Tricholoma terreum Schaeff.	*Agaricus terreus*	Wollaston (1807).
Tuber sp.	*Tuber* sp.	Tulasne and Tulasne (1851).
FUNGI OF DOUBTFUL IDENTITY		
Tricholoma graveolens (Pers.) Quel.	*Agaricus graveolens*	Way (1847).
Tricholoma gambosum Fr.	do	Do.
Hydnum cyathiforme Schaeff.	*Hydnum tomentosum*	Ludwig (1906).
Hydnum candicans Fr.	do	Do.
Caldesiella ferruginosa Sacc.	do	Do.
	Agaricus multifidus	Jorden (1862), Ritzema Bos (1901).

TYPES OF FAIRY RINGS

The present paper is concerned only with fairy rings produced as a result of the growth of fleshy fungi. When the fungi are in fruit, these rings are easily distinguished by the more or less regular arrangement of the fruiting bodies (Pl. 13, A). At other times the ring is easily distinguished by the appearance of the natural vegetation (Pl. 13, B). The differences in appearance of the vegetation in the ring as compared with that outside consist principally in a deeper color, due largely to greater chlorophyll content of the plants and in a more luxuriant growth, and in certain cases in a zone of bare ground or dead vegetation near the outer edge of the ring.

Before taking up a detailed description of the various types of rings found in eastern Colorado it seems desirable to review briefly the descriptions already published.

Hutton (1790) described a ring as consisting of three tracks, of which the first was a zone of dead or withered grass; the second lay just within and ran parallel to the first and appeared as a black zone of rotten grass; and the third, a dark-green zone of grass occurred partly on the black zone of rotten grass, but mostly on a smaller zone which had been formed the year preceding.

Practically every writer on this subject has included in his account a description of the rings. Few of these added materially to the description given by Hutton.

Westerhoff in 1859 (*in* Ritzema Bos, 1901) distinguished fairy rings formed by fungi and those formed by other causes. The fungus rings formed more or less complete circles, extending externally every year. They consisted of a zone of luxuriant grass of a dark-green color, surrounded by a circle of mushrooms (about August) and this in turn surrounded by a circle of withered grass. The inside of the ring appeared the same as the outside.

Jorden (1862) called attention to the green or brown rings and irregular dead patches, which were known as fairy rings.

Buckman (1870) and Kuperus (1876) described rings as formed of two bands, the inner one of fresh, green, luxuriant grass, and the outer

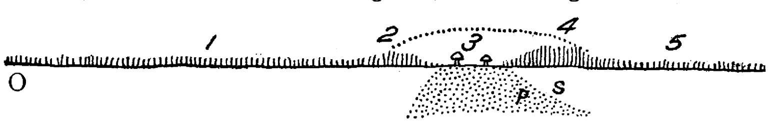

FIG. 1.—A sketch of a fairy ring produced by *Marasmius oreades*. The center of the circle is represented by O. The vegetation in the central part of the circle is represented at 1; the inner stimulated zone at 2, a bare zone at 3; and the outer stimulated zone at 4. The normal vegetation is shown at 5. The mycelium is represented by the dotted portion. The dotted line passing from zone 2 to 4 indicates the relative plant growth during the early spring when water is abundant (from Molliard, 1910).

one of more or less brown herbage or bare soil. Buckman stated further that the fungi appeared in this outer ring. He also described rings which consisted of only the fresh green ring and often produced no fungi.

Rings consisting of an outer dark-green zone, an intermediate yellow zone in which the grass was dead, and an inner green zone were described by Van Tieghem (1884, p. 1044–1045). In certain years the outer green band showed a large number of fungus fruits.

Sorauer (1886, p. 270–272) stated that the rings usually consisted of a green ring, and that it is only during an exceptional year that fungus fruiting bodies occur, while Stahl (1900, p. 666–667) described a ring distinguished by tall and robust plants of *Geranium robertianum*.

Complete rings so bare of grass as to resemble footpaths, formed by *Lycoperdon cyclicum* on a bowling green, were described by McAlpine (1898).

Ballion (1906) gave detailed descriptions of rings formed by *Marasmius oreades*, *Tricholoma georgii*, *Psalliota arvensis*, *Lycoperdon pratense*. These were grouped on the basis of (1) the place in the ring occupied by the fruiting bodies; (2) whether the vegetation was killed.

A ring of *Marasmius oreades* in the month of September was described by Molliard (1910, p. 63, fig. 1) as follows: There were three distinct zones: Beginning at the center (o, fig. 1) the first zone was an internal one (2) where the phanerogamic vegetation contrasted sharply with the normal; the second zone (3) a middle one where the herbage was withered and where the fruits of *M. oreades* occurred; and finally an external zone (4) larger than (2) the internal zone, where the vegetation was greener and taller than the inside (1) or the outside (5).

Münch (1914) described and illustrated a ring formed by *Agaricus* (*Clitocybe*) *maximus* which had a stimulated zone outside as well as inside a well-defined dead zone. It differed from the rings described by other investigators in that the dead zone was lined with fruiting bodies both on the exterior and interior sides.

Fairy rings caused by fleshy fungi may be divided into types on the basis of their effect on the vegetation. It is apparent from a review of the literature that the effect of the various fungi on the vegetation varies greatly in different locations as the probable result of the different climatic and weather conditions.

In eastern Colorado the following types of fairy rings may be distinguished: (1) Those in which the vegetation is killed or badly damaged, caused by *Agaricus tabularis;* (2) those in which the vegetation is only stimulated, caused usually by species of Calvatia, Catastoma, Lycoperdon, marasmius, etc.; and (3) those in which no effect can be noted in the native vegetation, caused by *Lepiota* spp.

RINGS MARKED BY A ZONE OF DEAD VEGETATION

RINGS FORMED BY AGARICUS TABULARIS

The rings formed by *Agaricus tabularis* Peck vary in size from a few meters to 70 meters across. These rings are often complete and circular, the advance in all directions having been nearly uniform (Pl. 13, A; 18; 20; 30, A). More often, however, the ring is broken at certain points, and the larger rings are usually formed by a series of arcs which do not come into contact with each other but which show approximately equal radii (fig. 2).

In figure 3 is given a diagram and in figure 4 a bisect of a typical ring formed by *Agaricus tabularis*. At A the zones are shown as they are distinguished during a period favorable for the growth of the fungus and the production of fruiting bodies. (Pl. 13, A; 14, A; 19.) The ring consists of a series of three zones surrounding an area of normal short grass sod, which constitutes the inside of the ring (1). Next to this area occurs a broad zone differing from the natural sod in botanical composition, in the more luxuriant growth, and in the deeper green color of the vegetation. This is the inner stimulated zone (2). This wide green zone is the most prominent part of the rings in spring or in wet seasons. The bare zone (3) is not as broad as the inner stimulated zone and is somewhat more irregular. In this zone the vegetation is often entirely dead, but in many

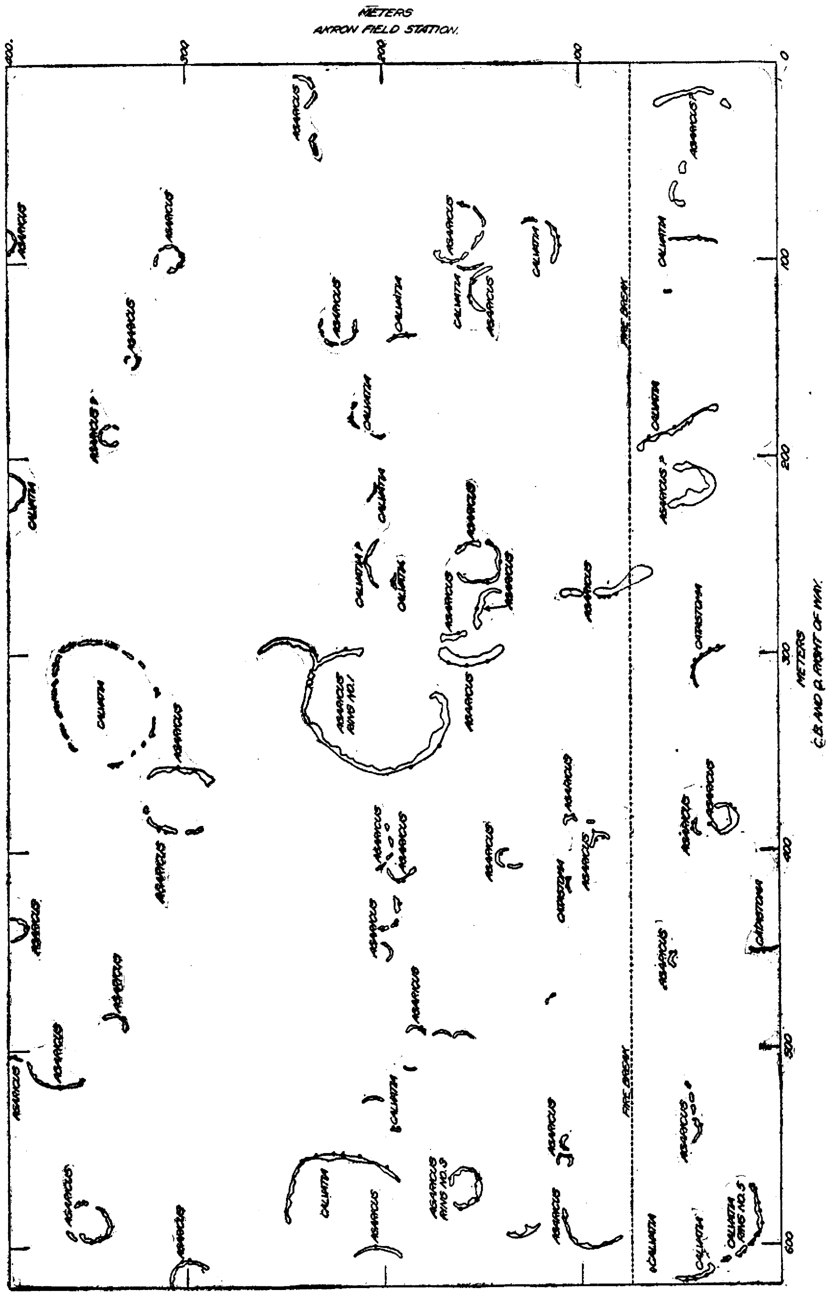

FIG. 2.—A map of an area of 400 by 620 meters, lying just west of the experiment station and north of the Chicago, Burlington & Quincy R. R. near Akron, Colo. The dotted line represents a fire break plowed each fall and of about 2 meters' width. This area includes a total of 62 rings or fragments of rings: 35 are *Agaricus tabularis*, 14 *Calvatia cyathiformis*, 3 *Catastoma subterraneum*, and 10 are unidentified rings. No rings of *Agaricus campestris* were noted in this section, although many grow at other places on the plains. From 0.5 to 1 per cent of the total land area here shown lies within the zone of influence of these fairy rings. The fruiting bodies at the time the map was made are represented by dots.

cases a few very poor perennials or short-lived annuals may be found. This zone is the distinguishing feature late in summer and fall or in dry seasons. If rains are frequent, scattered annuals succeed fairly well even on this area. Beyond the bare zone there occurs a rather narrow zone, the outer stimulated zone (4), resembling somewhat the inner stimulated zone, but being for the most part made up entirely of plants which characterize the native sod. The sporophores occur in this zone, near the outer edge. Outside this zone normal native short grass is found (5).

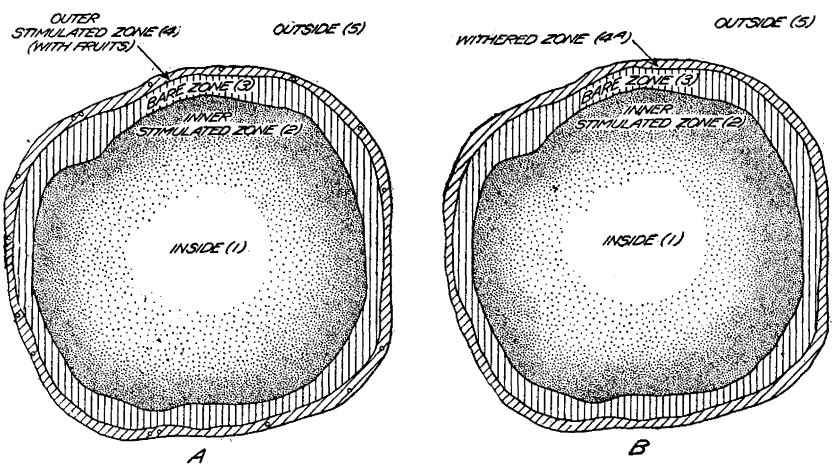

FIG. 3.—A sketch showing the different zones in a typical ring formed by *Agaricus tabularis*. At A the appearance of the ring is shown during a period of ample moisture supply. At B the appearance during a period of deficient moisture supply. The vegetation on the inside (1) is normal. In the inner stimulated zone (2) the greatest stimulation occurs near the bare zone. The bare zone (3) is usually devoid of vegetation, or contains only scattered plants. The outer stimulated zone (4) contains the fruiting bodies of the fungus and differs from the vegetation outside only in color and in more luxuriant growth; outside, the vegetation is normal (5). In B the same zones are shown as in A, except the outer stimulated zone which is here shown as the withered zone (4*a*). In this zone the plants not only wither but with continued droughts will die, and the area of this zone be added the following year to that of the bare zone.

At B the zones are shown as they appear during a period not favorable to fungus growth. During the late summer, when the moisture supply is deficient, or during a dry year following a wet year (Pl. 16) the ring presents a very different appearance from that described above. The inner stimulated zone (2) ripens or dries up as dry weather comes on and usually presents a brown, dead appearance, although the perennials remain alive in a dormant condition. If the season is dry, this zone (2), while noticeably different from the natural sod inside (1), does not show the luxuriant growth so characteristic of a wet year. During a dry year the bare zone (3) is unusually prominent, since not even the short-lived annuals appear, and the zone is named from its appearance during drouth periods. Such periods are characteristic of eastern Colorado. The withered zone (4a) is characterized by the dry vegetation, which during the more favorable period had marked the outer stimulated zone (4). During a dry year the short grass in this area is withered and often perfectly air-dry when the adjacent sod is still green.

RINGS MARKED ONLY BY A ZONE OF STIMULATED VEGETATION

Most of the fungi forming fairy rings in eastern Colorado produce only a temporary stimulating effect on the vegetation. In this group, therefore, the presence of fungi is indicated by an increase in the size, vigor, and chlorophyll content of the annuals and of the perennial grasses.

RINGS FORMED BY CALVATIA CYATHIFORMIS

A large number of the rings marked only by a zone of stimulated vegetation are produced by *Calvatia cyathiformis* Bosc (fig. 5, 6). They are usually much less conspicuous than those formed by *Agaricus tabularis.*

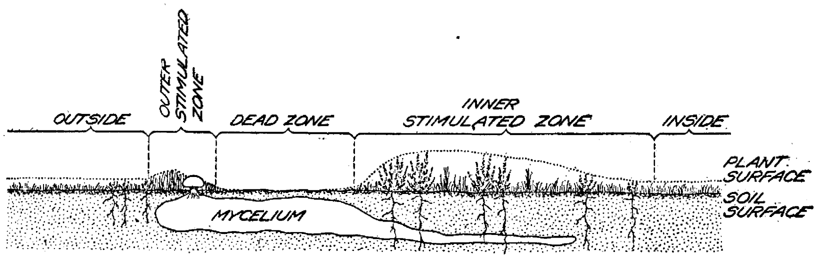

FIG. 4.—A bisect of the *Agaricus tabularis* ring shown in figure 3 at A. The vegetation on the inside and outside does not differ noticeably. The outer stimulated zone in which the fungus fruits are produced is separated from the inner stimulated zone by a bare zone in which plants are only occasionally found. The distribution of the mycelium in the soil is also indicated in the illustration.

In size they are often much larger. Several rings have been observed which exceed 200 meters in diameter (Pl. 24,B). In periods when the rings are not marked by fruiting bodies these rings can be distinguished from Agaricus by the sterile bases of the fruits of *Calvatia cyathiformis* which remain on the ground from one year to another, or by the natural vegetation which usually presents a stimulated appearance, but seldom, if ever, is damaged by the presence of the fungus. The annuals in the rings, which grow much taller than in the adjacent areas, are prominent both during their period of rapid growth and after they have ripened, at which time the rings appear as dark-yellow or brown circles on a uniformly light-green short-grass cover.

A sketch of a ring formed by this fungus is shown in figure 5. The first crop of fruiting bodies occurs at the outer edge of the stimulated zone. The vegetation in this zone consists of the same species as the native sod, but the growth is more luxuriant (Pl. 25,A). This is especially noticeable in the short-lived annual plants which stand up prominently above those in the surrounding sod. If the season is favorable and a second crop of puffballs is produced, they appear outside in advance of the stimulated zone (Pl. 26, A).

RINGS FORMED BY CALVATIA POLYGONIA

The giant *Calvatia polygonia* Lloyd is somewhat less abundant on the Great Plains than the one just discussed. It occurs frequently in eastern Colorado and forms large rings not differing essentially from those described for *Calvatia cyathiformis*. The rings formed by this fungus are usually intermediate in size, one ring having been noted with a diameter of 100 meters (Pl. 28, B).

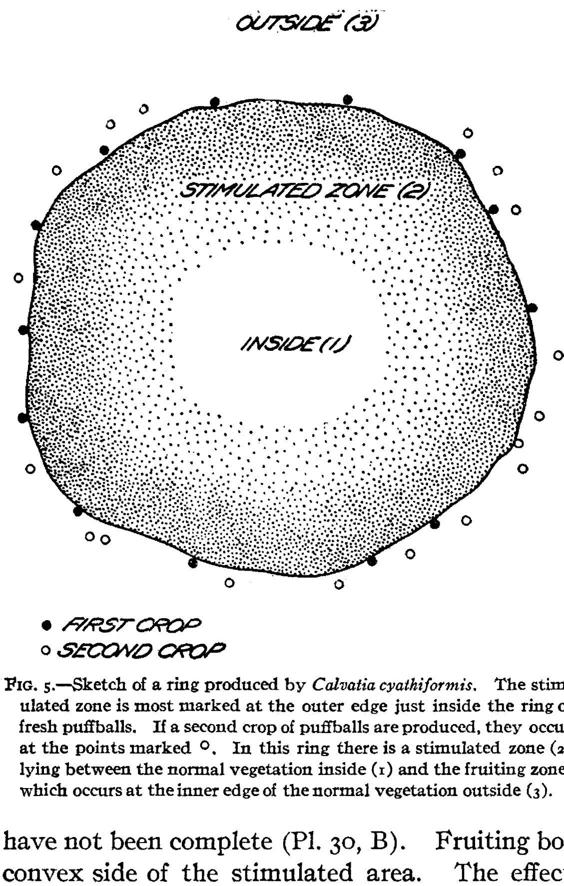

FIG. 5.—Sketch of a ring produced by *Calvatia cyathiformis*. The stimulated zone is most marked at the outer edge just inside the ring of fresh puffballs. If a second crop of puffballs are produced, they occur at the points marked ○. In this ring there is a stimulated zone (2) lying between the normal vegetation inside (1) and the fruiting zone, which occurs at the inner edge of the normal vegetation outside (3).

RINGS FORMED BY CATASTOMA SUBTERRANEUM

The interesting fungus *Catastoma subterraneum* (Pk.) Morg., the fruiting bodies of which develop underground and do not appear on the surface until after they have broken loose from their attachment, forms noticeable rings indicated by a stimulation of the native plant cover. The rings thus far noted by the writers have not been complete (Pl. 30, B). Fruiting bodies are formed near the convex side of the stimulated area. The effect on the native vegetation is the same as in the case of *Calvatia cyathiformis*, but the stimulated zone is even narrower.

RINGS FORMED BY OTHER FUNGI

Lycoperdon gemmatum and *L. wrightii*, which occur more commonly on cultivated and disturbed land, indicate little effect in stimulating the vegetation. *Calvatia fragilis* Vitt, *Marasmius oreades* (Fr.) Bolt, *Agaricus campestris* L. (Pl. 28, A), and *Tricholoma melaleuca* (Pers.) Quel. occur rather commonly in the short-grass vegetation and form rings marked by a stimulated area or by the occurrence of the fruiting bodies. The rings are usually small, seldom exceeding 6 to 10 meters.

RINGS WHICH PRODUCE NO NOTICEABLE EFFECT ON THE NATURAL VEGETATION

A single ring formed by *Lepiota morgani* Pk. was noted in the bunch-grass vegetation near Yuma, Colo. (Pl. 26,B; 27,C). The ring, approximately 24 meters in diameter, was composed of about 63 fruits (fig. 7). No effect could be noted on the vegetation. It is possible, however, that if this fungus had developed on the hard land in the short-grass cover, the effect would have been more noticeable.

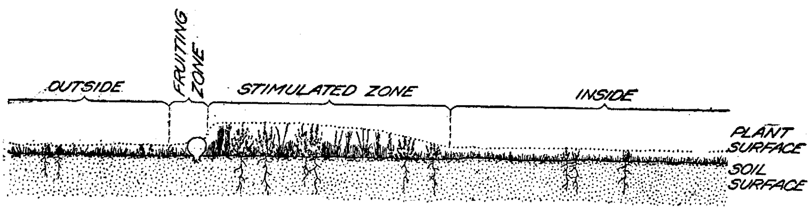

FIG. 6.—A bisect of a ring sketched in figure 5. In the case of *Calvatia cyathiformis* the distribution of the mycelium can scarcely be detected in the soil. The stimulated zone lies just inside the zone of fruiting bodies.

DISTRIBUTION OF FAIRY RINGS

Fairy rings occur for the most part in grass lands, but have been recorded in many cases in forests. Most of the investigators refer to them as having been formed in grassy areas and marked by the more luxuriant growth of grasses. The following authors discuss rings in this type of vegetation: Bradley (1717, p. 122–123) Hutton (1790), Wollaston (1807), Dutrochet (1834, 1837, p. 179–181), De Candolle (*in* Way, 1847), Way (1847), Westerhoff in 1859 (*in* Ritzema Bos, 1901), Berkeley (1860), p. 41), Jorden (1862), Cooke (1866), Lees (1869), Buckman (1870), Gilbert (1875), Kuperus (1876), Lawes, Gilbert, and Warington (1883), Van Tieghem (1884, p. 1044–1045), Sorauer (1886, p. 270–272), Treichel (1889), Olivier (1891), McAlpine (1898), Coville (1897, 1898), Atkinson (1900), Williams (1901), Ritzema Bos (1901), Beille (1904, p. 380–381), Baillion (1906), Molliard (1910), Massart (1910), Bayliss (1911), Münch (1914), and Ramaley (1916).

The following dealt with fairy rings in forests or about trees: Tulasne and Tulasne (1851, p. 157–158), Stahl (1900, p. 666–667), Thomas (1905), Ludwig (1906), Reed (1910), and Coulter, Barnes, and Cowles (1911, p. 807).

Dutrochet (1837, p. 179–181) called attention to the fact that rings develop most commonly on prairies that are not very fertile and where the grass is short and yellow. Gilbert (1875) stated that it is known that fairy rings occur chiefly, though not exclusively, on poor pastures, and that they are discouraged by especially high nitrogenous manuring. Ritzema Bos (1901) stated that the best fairy rings are produced during rather dry seasons, and that mushrooms usually occur in meadows where the organic matter is not abundant.

On the Great Plains fairy rings have been noted in all sections from Texas to Montana. Their abundance in certain areas is illustrated in figure 2. This map covers an area of three-fourths of a mile by one-half a mile of unbroken native sod lying just west of the Akron experiment farm, near Akron, Colo. A total of 62 rings or fragments of rings is shown on this map. From 0.5 to 1 per cent of the total soil area lies within the zone of influence of these rings. This area contains 35 Agaricus rings, 14 Calvatia rings, 3 Catastoma rings, and 10 unidentified rings. Throughout the whole of eastern Colorado, especially on the "hard" land (characterized by the pure short-grass cover), fairy rings occur often in great abundance. Many other areas might have been chosen which would show an equal or possibly even greater number of rings.

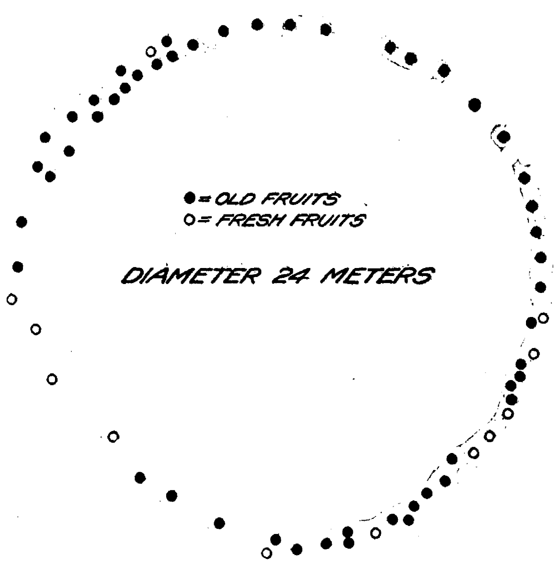

FIG. 7.—A sketch of a fairy ring formed by *Lepiota morgani* southeast of Yuma, Colo. No effect could be noted on the vegetation.

About one-half of the area shown in this map was plowed in the fall of 1915 and seeded to Turkey wheat. During 1916, an exceptionally dry year, the area was remapped. The results of this remapping are shown in figure 8.

CAUSE OF ADVANCE

Hutton (1790) noted the regular annual progression of fairy rings, but Wollaston (1807) was the first to discuss the cause of this progression. He came to the conclusion that the ring was formed by a progressive increase from a central point due to the exhaustion in the central area of some particular "pabulum" necessary for the further growth of the fungus; hence, the new growth of the fungus "roots" extended solely in the opposite direction—that is, outward. He confirmed his theory by the observation that, where two circles met, both were obliterated at the point of contact, and said:

The exhaustion occasioned by each obstructs the progress of the other, and both are starved.

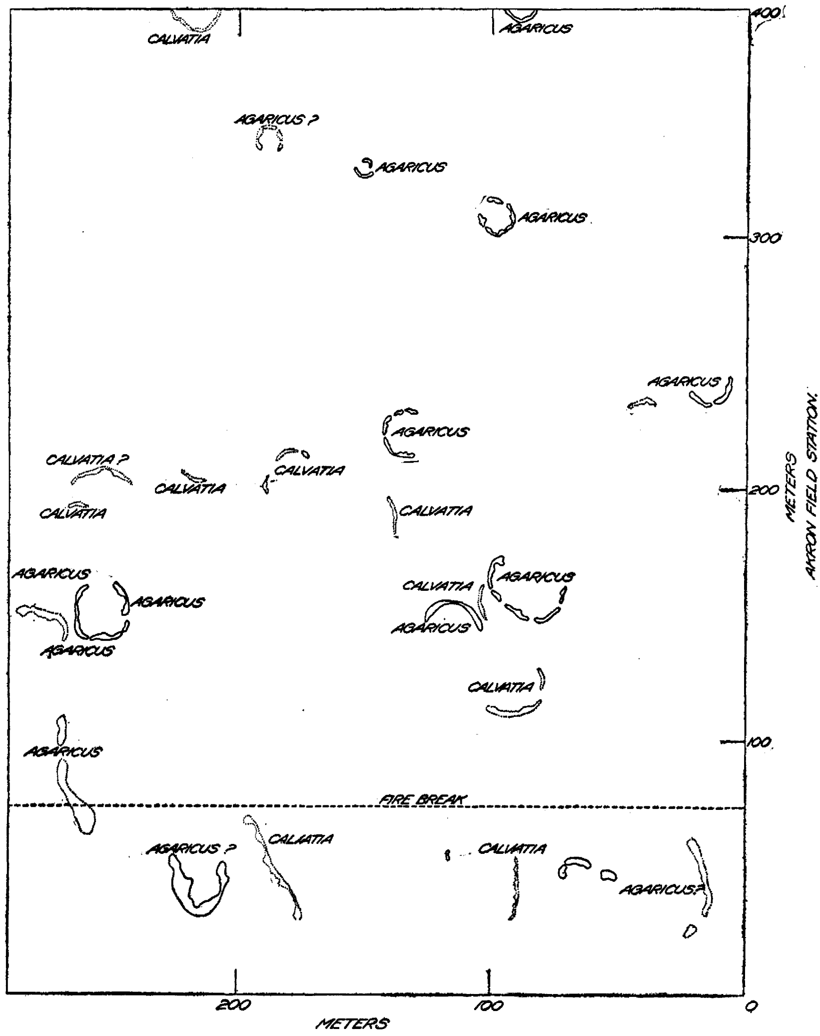

FIG. 8.—Remapped area shown in figure 2. During the fall of 1915 a portion of the area mapped in figure 2. was plowed and planted to fall wheat. During June, 1916, the area was remapped. This area is 400 by 290 meters and comprised the portion lying next to the experiment station grounds. A comparison with figure 2 will show that none of the Calvatia rings could be detected in the wheat crop the following year. Of 12 Agaricus rings mapped in 1915, 9 were easily detected in the wheat field in 1916.

Way (1847, p. 43) thought that—

The theory of de Candolle, that these rings increase by the excretions of these fungi, being favorable for the growth of grass but injurious to their own subsequent development on the same spot, was insufficient to explain the phenomena.

That there was no further fungus growth within the ring he attributed to the competition with a vigorous crop of grass.

Westerhoff in 1859 (Ritzema Bos, 1901) attributed the centrifugal growth of the mushrooms to excrements of the roots of the mushrooms.

Berkeley (1860, p. 41) noted the tendency of fungi to assume a circular growth not only when the spawn was perennial but where the whole period of existence of the fungus amounted to only a few days or weeks. Fairy rings originated from a single spore, the growth from which rendered the soil unfit for further fungus growth. The rings extended outward until interrupted.

The various investigators following this period ascribed the cause of advance to those already recorded. Ritzema Bos (1901) likened the advance of a fairy circle to the progressive advance of a flame which results from dropping a match in dry grass, and which will spread continually outward.

Reed (1910) stated that the tannin of the bark of a hemlock tree marking the center of a fairy ring had caused the death of the ring on the downhill side. But Coville (1898) found the rings uniformly broken on the downhill side, which suggests the harmful influence of the decomposition substances which are washed toward the lower side.

Investigators differ as to the exact cause of this outward growth, some attributing it to the exhaustion of the nutrient materials of the soil, others attributing the cause partially to the fact that the active mycelium occurs only on the outside of the ring, and that the portion of the mycelium on the inside is already old or dying. That the mycelium grows outward from a central point and continues to grow outward is no more strange than that the horizontal roots grow out from the tree and keep on growing out instead of back toward the trunk. The fact that the filaments grow into virgin soil by growing outward would favor the growth in that direction.

Where fungus fairy rings occur, the soil is usually rather low in organic matter. The growth of the saprophytic fungus probably consumes the available supply of organic matter. In the case of the *Agaricus tabularis* ring this is replenished by the death of the grass cover and by the subsequent increase in growth of annuals and short-lived perennials, which die and leave their root systems as available organic matter. Determinations of organic matter do not therefore show a marked difference outside or inside the fairy ring. The active fungus filaments are always on the outer edge, and a turning back into the central area would require passage through from 1 to 5 meters of depleted soil or a continuance in a living condition for a period of several years in the same spot or soil mass. In addition to these reasons why progression should be outward, observations are numerous of the tendency of fungus filaments or even roots of growing plants to distribute themselves rather evenly into new soil areas. When fungus filaments approach each other, they turn aside

(Fulton, 1906). This may be due to chemotropic stimulation or to the more obvious fact that food material or water is usually more abundant in the new soil. The high content of ammonia and nitrates in the soil

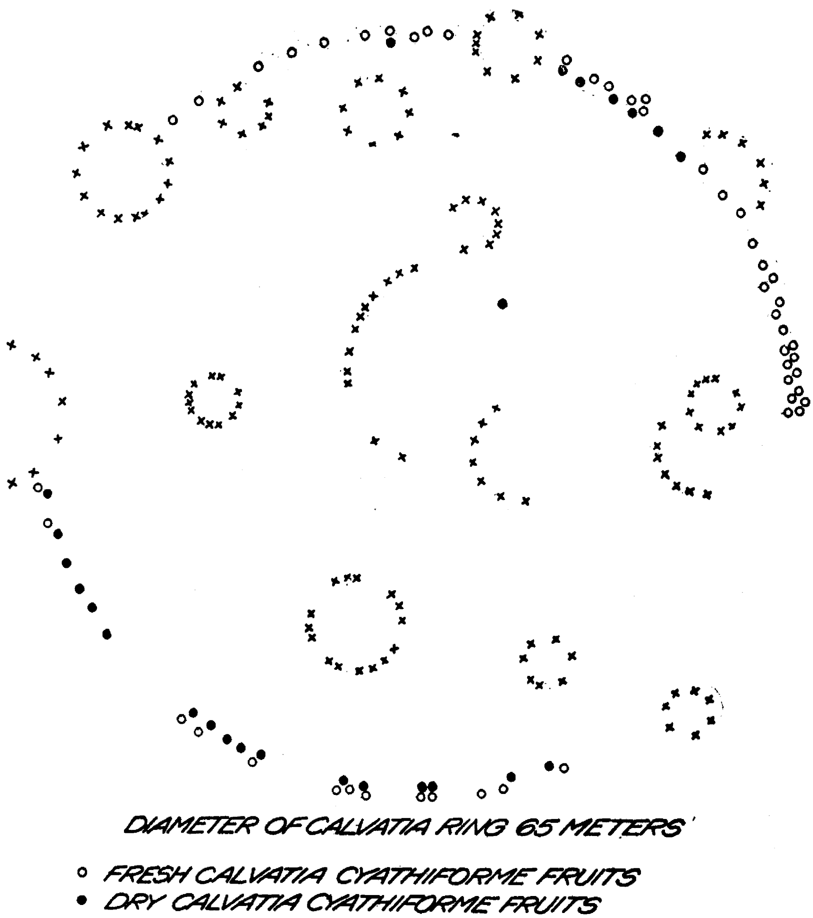

Fig. 9.—A ring formed by *Calvatia cyathiformis*, almost complete and 65 meters in diameter. The ring contained 50 fresh fruiting bodies and had apparently produced an earlier crop of 54 puffballs. This ring occurred in an area in which a great number of small rings produced by *Agaricus compestris* were found. These rings seem to have interrupted the Calvatia rings at all points except on the upper right-hand side. At no place is there evidence that the *C. cyathiformis* displaced *A. campestris*, although a possible condition of this kind is indicated on the upper right-hand portion of the figure. This ring was mapped northeast of Yuma, Colo., on June 29, 1916. It should be noted that, although Calvatia and Agaricus fruited abundantly in the region about Yuma and on the Wray Divide in 1916, no fruiting bodies were produced at Akron. The records in Table II are for the vicinity of Akron and are not general for the whole eastern portion of the State.

occupied by the older portion of the mycelium may also play a part. That rings do not continue when they come in contact with each other has been noted repeatedly. The inside of large rings of one species is often occupied with many smaller rings of another species (fig. 9), and in one case a ring of *Calvatia cyathiformis* had five large fruiting bodies in the area inside the ring. Two of these fruiting bodies were near the center of the ring, while three were situated about midway between the center and the stimulated zone. But the period of time which had elapsed since the soil mass was infected by the fairy-ring fungus may have been sufficient for the organic matter and the other conditions of the soil to have again become normal.

EFFECT OF SOIL AND WEATHER CONDITIONS ON THE PRODUCTION OF FRUITING BODIES

The production of fruiting bodies seems to be dependent largely on the soil and weather conditions. Jorden (1862) called attention to the influence of weather conditions, especially warmth and moisture, on the production of fruiting bodies in fairy rings. One ring of *Agaricus giganteus* fruited only once during a period of 50 years' observation.

In Table II are shown the dates on which the fungi fruited abundantly in the vicinity of Akron, Colo., during the years 1907–1916, inclusive. These records, taken from field notes, are probably complete, except for the occasional production of fruiting bodies in a small area under abnormally favorable conditions caused by local showers or drainage water.[1]

TABLE II.—*Dates on which fungi have been noted in fruit in the fairy rings at Akron, Colo.*

Year.	Date of occurrence of fruiting bodies.		
	Agaricus tabularis.	*Calvatia cyathiformis.*	*Calvatia polygonia.*
1907	June 21	July 26	July 20.
1908			
1909	June 3–19	June 12–19 July 13–17	July 6. August 10.
1910		August	August.
1911			
1912		June	September 13.
1913			
1914		June 21	
1915	June 5–24 August 16–20	June 14–24 August 16–20	June 21.

Calvatia cyathiformis was noted in six of the nine years, *Calvatia polygonia* in five, and *Agaricus tabularis* in but three. *A. tabularis* fruited earlier in the season than the other fungi. During 1909 and 1915, when conditions were most favorable for the growth of these fungi, *A. tabularis* fruiting bodies appeared early in June, followed about 10 days later by fruiting bodies of *Calvatia cyathiformis*. A second and very light crop

[1] In 1912 the writers were absent during the latter part of May and the greater part of June, and no records were secured until June 19, after which date fungi were not noted. Mr. Robert D. Rands, who assisted in the alkali and drought resistant plant investigations at Akron, Colo., photographed a ring of *Calvatia cyathiformis* early in June. It seems improbable that Agaricus fruited during this year, since only a few Calvatia fruits and no fruits of Agaricus were noted by Mr. Rands.

of each of these fungi occurred on August 16, 1915, following a rain on August 14 of 0.43 inch. Similarly *C. cyathiformis* produced on July 13, 1909, a second crop following a series of heavy rains (2.80 inches) on July 7–9.

Calvatia polygonia fruited later in the season. The earliest record of its occurrence was June 21, 1915. In 1909 it was found in fruit on July 6 and again on August 10. It did not fruit as freely as did *Calvatia cyathiformis*, and often the rings produced only one or two fruiting bodies at a time.

In Table III is shown a summary of the weather conditions [1] for each of the years here considered, with the exception of 1907, during which year no determinations are available. The data are summarized for the months of May, June, July, and August.

Soil moisture was the chief factor in controlling the fruiting of these fungi. If during May and June the soil of the first and second foot was moist throughout, these fungi fruited rather abundantly. If the soil was dry even during a part of this period, the fruiting bodies were not produced. These data are not taken from moisture determinations in the fungus ring but from determinations in the typical short-grass sod. As will be shown later, the moisture conditions in the Agaricus rings are not as favorable as those shown in this table.

In 1909 and 1915 the soil of the first and second foot was moist during the month of June, and the fungi fruited abundantly throughout this period. In 1912 soil moisture conditions seem to have been favorable during June. The failure of *Agaricus tabularis* to fruit at this time may have been due to the very extreme conditions of drouth during the preceding season. In 1914 *Calvatia cyathiformis* fruited sparingly but *A. tabularis* produced no fruiting bodies. The impervious nature of the soil in Agaricus rings probably explains the absence of fruiting bodies of this fungus in 1912 and 1914, following the dry years 1911 and 1913. On the basis of soil moisture, 1909 and 1915 were the most favorable years.

The rainfall was heavier in 1909 and 1915 than in any other year. The combined rainfall in May and June, the period during which it would be most important as a factor in fungus growth, was especially low in 1910, 1911, 1913, and 1916, the years during which fungi did not fruit.

The number of rainy days gives a better idea of the general conditions of humidity than does the amount of rainfall. Rainy days were more numerous during May, June, July, and August in 1915 than during any other year, including 1909, when a good crop was produced. In the period for 1915 more than half the days were rainy. Evaporation was lowest in 1915. A comparison of the evaporation rate in June, 1915, with that of the same month in 1909 shows conditions to have been

[1] For the weather data here recorded the writers are indebted to Dr. L. J. Briggs, Biophysicist in Charge of the Office of Biophysical Investigations, Bureau of Plant Industry.

much more extreme in 1909 than in 1915. The years 1908, 1911, 1913, and 1916 were the most extreme, to judge from the evaporation rates. It was during these years that no fruiting bodies were observed.

TABLE III.—*Weather and soil conditions during the months of May to August for the years 1908 to 1916 at Akron, Colo.*[a]

Condition and month.	1908	1909	1910	1011	1912	1913	1914	1915	1916
Evaporation (inches):									
May	7.709	6.825	5.797	7.323	7.097	5.835	5.608	5.033	7.811
June	8.637	7.003ac	8.722	9.753	6.750c	8.178	7.509c	5.883ac	7.979
July	8.474	9.396c	9.763	9.774	7.618	9.259	8.654	6.660	11.116
August	7.826	8.538	7.142c	8.944	7.048	9.302	8.364	5.820ac	7.216
Mean	8.162	7.941	7.856	8.949	7.128	8.144	7.534	5.849	8.531
Rainfall (inches):									
May	3.30	1.87	2.06	1.15	2.86	1.44	1.46	4.13	2.24
June	2.37	3.32ac	1.38	1.48	3.39c	1.35	3.54c	3.75ac	2.09
July	2.42	4.61c	1.47	1.34	3.58	1.85	1.66	1.10	1.77
August	1.47	3.77	3.72c	1.30	1.58	1.14	1.05	3.51ac	2.82
Mean	2.39	3.39	2.16	1.32	2.60	1.45	1.93	3.12	2.23
Rainy days (trace or over):									
May	9	12	13	12	15	10	12	16	12
June	18	15ac	5	10	11c	12	11c	19ac	10
July	12	9c	5	13	17	10	17	21	13
August	12	6	12c	10	11	7	14	17ac	15
Mean	13	11	9	11	14	10	14	18	13
Mean temperature (°F.):									
May	55	52	53	58	55	57	57	52	55
June	64	64ac	67	70	63c	67	68c	60ac	64
July	70	71c	74	70	70	72	72	67	75
August	69	72	67c	69	69	75	71	64ac	69
Mean	65	65	65	67	64	68	67	61	66
Soil temperature (°F.):									
May	74+	57	59	62	60	63	63	56+	60
June	74	67ac	63	77	68c	75	76c	71+ac	73
July	77	64+c	85	80	76	80	81	74	81+
August	75	....	77c	77	76	83	79	71ac	77
Mean	75+	63+	71	74	70	75	75	71+	75+
Maximum air temperature (°F.):									
May	90	85	87	91	92	91	85	88	70
June	93	93ac	95	98	89c	97	93c	82ac	80
July	94	94c	100	95	96	103	96	95	93
August	98	95	95c	97	96	98	101	94ac	83
Minimum air temperature (°F.):									
May	24	24	29	28	28	31	32	27	41
June	41	41ac	32	43	37c	37	38c	35ac	49
July	42	51c	51	46	47	43	49	40	60
August	46	51	31c	41	48	53	42	39ac	56
Number of days during which available soil moisture was recorded in the first foot:									
May	....	....	....	....	....	19	31	31	8
June	....	30ac	17	10	30c	2	22c	30ac	23
July	7	18c	2	0	13	8	11	14	0
August	....	24	22c	6	12	0	0	31ac	2
Number of days during which available soil moisture was recorded in second-foot:									
May	....	....	....	....	....	0	31	31	31
June	....	30ac	23	0	30c	0	30c	30ac	30
July	....	19c	0	0	23	0	14	30	23
August	....	0	0c	0	0	0	0	30ac	0

[a] += Record incomplete; a= *Agaricus tabularis;* c= *Calvatia cyathiformis* in fruit at sometime during the month.

The mean temperature of the soil during May and June, 1909, was 57° and 67° F., respectively. During 1915, when the fungi fruited abundantly, the soil temperature records were not complete, but indicate that conditions were nearly the same as in 1909, the values being 56° and 71°, respectively. The mean air temperatures did not vary markedly during the different years, except that 1915 was cooler than the other years. This is indicated in the maximum and minimum as well as in the mean temperatures.

WEATHER AND SOIL CONDITIONS DURING THE FRUITING PERIODS

The conditions during and preceding the principal fruiting periods in 1909 and 1915 are given in Table IV. The conditions during the period of fruiting are of interest in connection with the character of the fruiting bodies and the length of the fruiting period. The conditions immediately preceding determine whether or not fruiting bodies will be produced.

TABLE IV.—*Weather conditions for 10 days preceding and during the fruiting period of Agaricus tabularis and Calvatia cyathiformis*

Species and period.	Daily evaporation.	Daily rainfall.	Climatic conditions.					Soil moisture conditions.	
			Percentage of days with rain.	Temperature (°F.).					
				Soil.	Air.			First foot.	Second foot.
				Mean.	Mean.	Maximum.	Minimum.		
Agaricus tabularis:	*Inch.*	*Inch.*							
Fruiting period, June 3–19, 1909.	0.218	0.29	65	65	62	91	41	Moist...	Moist.
Previous 10-day period, May 25–June 3, 1909.	.197	.08	60	57	55	85	36	...do.....	Do.
Fruiting period, June 5–24, 1915.	.208	.13	60	....	60	82	35	...do.....	Do.
Previous 10-day period, May 26–June 4, 1915.	.132	.25	80	....	54	71	37	...do.....	Do.
Fruiting period, Aug. 16–20, 1915.	.199	.06	80	71	63	82	49	...do.....	Do.
Previous 10-day period, Aug. 6–15, 1915.	.204	.12	80	71	57	82	35	...do.....	Do.
Calvatia cyathiformis:									
Fruiting period, June 12–19, 1909.	.232	.04	50	67	64	83	46	...do.....	Do.
Previous 10-day period, June 2–11, 1909.	.192	.28	80	63	60	91	41	...do.....	Do.
Fruiting period, July 13–17, 1909.	.294	0	0	59	71	91	54	...do.....	Dry.
Previous 10-day period, July 3–12, 1909.	.293	.28	50	65	78	90	51	Dry to moist.	Moist to dry.
Fruiting period, June 14–24, 1915.	.186	.04	64	[a] 70	62	82	46	Moist...	Moist.
Previous 10-day period, June 4–13, 1915.	.234	.26	70	....	56	82	35	...do.....	Do.
Fruiting period, Aug. 16–20, 1915.	.199	.06	80	71	63	82	49	...do.....	Do.
Previous 10-day period, Aug. 6–15, 1915.	.204	.12	80	71	57	82	35	...do.....	Do.

[a] Record incomplete.

Agaricus tabularis fruited only once in 1909, the fruiting period extending over 17 days. At this period the soil-moisture determinations in short-grass land showed available moisture in both the first and second foot, and the mean soil temperature of 65° F. The mean air temperature was a little lower, 62°, and the range in air temperature from 41 to 91°. The daily evaporation rate was relatively high, amounting to 0.218 inch from the free-water surface of a 6-foot tank. The rainfall averaged 0.29 inch per day, or a little greater than the evaporation.

In 1915 *Agaricus tabularis* fruited twice, the June period covering 20 days and the August period only five days. Soil-moisture conditions were favorable during both of these periods. Conditions of evaporation were similar. Although but a small amount of rain fell during the late period, the percentage of days with rain was very high. Soil temperature was high during the late period. During the early period continuous soil temperature records were not available, but occasional records showed the temperature to have differed but little from the temperature of the early period in 1909. The air temperatures did not differ markedly from those of 1909, except that the maximums were much lower for each crop. A comparison of the conditions in 1909 with those of 1915 shows only a slightly higher evaporation and higher maximum temperature in 1909. The effect of the more extreme conditions on the fruiting bodies of the fungi will be noted later.

Calvatia cyathiformis, which fruits later in the season, usually fruits during periods of higher evaporation and higher temperatures. In 1909 the first fruiting period extended over eight days. The mean soil temperature was a little higher then than during the Agaricus period and the evaporation a little more extreme, but the air temperature range not as great. Otherwise, conditions were similar. The second fruiting period came during July and lasted only five days. The soil temperature was unusually low, the air temperature reached its maximum on the last day of the period. Evaporation was high and there was no rain. The soil was rapidly drying off. This second fruiting period followed a rainfall of 2.39 inches on July 7. The soil of the first foot was moist, but that of the second foot dry during this period.

In 1915 the June fruiting period covered 11 days. The soil was moist at this time and the air temperature rather high, but the evaporation was unusually low. During this damp period with frequent rain and low evaporation the fruiting bodies were produced under conditions markedly different from those of 1909, in so far as aerial conditions are concerned. The second fruiting period covered only four days in August. The mean temperature of the soil was 71° F., although the air temperature was rather low. This period followed a period of rainy weather, as is shown by the 10-day period preceding. The evaporation was unusually low, and rain was recorded on four of the five days considered.

EFFECT OF WEATHER CONDITIONS ON THE CHARACTER OF THE FRUITING BODIES.

The effect of high temperature on the fruiting bodies is well known. Fruiting bodies which appear during damp, warm periods decay rapidly and are soon destroyed by maggots. On the other hand, those which appear during cool periods remain fresh for a much longer time.

On the Great Plains it often happens that a spell of wet weather will be followed by an exceedingly dry period in which the evaporation from the soil and transpiration from the plant surface is excessive. When the fruiting bodies of the fungus are produced during such a dry period, the shape and proportions of these bodies and the character of the top of the pileus are greatly modified. The fruiting bodies of *Agaricus tabularis* produced during a period of rapid evaporation have a very rough and scaly periderm, a thick, firm pileus, and a short, thick stipe. These present better herbarium material when dried in place than when dried in a drying oven. On the other hand, if the fruiting bodies are produced during a period of less excessive evaporation, the pileus is thinner and expanded, the stipe long, and the periderm often quite smooth. These decay rapidly, and are difficult to preserve. In 1909 the tops were mostly rough (Pl. 10, B, C). They were produced during a period of comparatively rapid evaporation. During the year 1915 the tops were either smooth or rough, depending upon the time of appearance and the exposure. The fruiting bodies produced among taller growing plants and grasses almost invariably had smooth tops (Pl. 11, A), while those which occurred in the open had rough tops (Pl. 11, B, C).

The *Agaricus tabularis* ring sketched in figure 10 was partly in a cornfield and partly in the open. The fruiting bodies developed in the cornfield were comparatively smooth on top, the pileus spread out very wide and thin, and the stipe comparatively long and slender, while the fruits produced in the short-grass sod had a thick, firm, pileus, rough on top, and a very short and stocky stipe. The differences were similar to those shown in Plates 11 and 12.

The amount of variation in the pileus is well illustrated by the fresh sporophores shown in Plates 10 and 11 and the dried sporophores shown in Plate 12. In Plate 12, A and B, the characteristic pileus of *Agaricus tabularis* is shown, while in Plate 12, C and D, this tabular structure is entirely lacking.

Duggar (1905), who has made an extensive study of wild and cultivated forms of Agaricus, calls attention to the great amount of variation produced in the different strains under different cultural conditions. This wide range of variation and the effect on morphology, color, etc., make doubtful the specific value of forms showing only slight morphological differences (Duggar, 1915).

It has been difficult to determine the number of distinct forms occurring as fairy rings in eastern Colorado. The first form to appear in the spring is *Agaricus tabularis*, ranging morphologically from typical *A. tabularis* to the smooth expanded type similar to *A. arvensis*. Later in the season, if moisture conditions are favorable, a series of smaller forms (*A. campestris*) appear which show almost as wide a range in morphological characters as does *A. tabularis*, but which are entirely distinct from the latter in time of appearance and in the character of the mycelium in the fairy ring. The mycelium is not dense in the soil. The whole plant is less vigorous, the fruiting bodies are smaller and of a more delicate texture. But in this group the fruiting bodies often become decidedly rough on top and present wide variability in the appearance either of the fresh or the dried forms. The appearance of the fairy rings produced by the *A. tabularis* group is entirely distinct from rings of the *A. campestris* group.

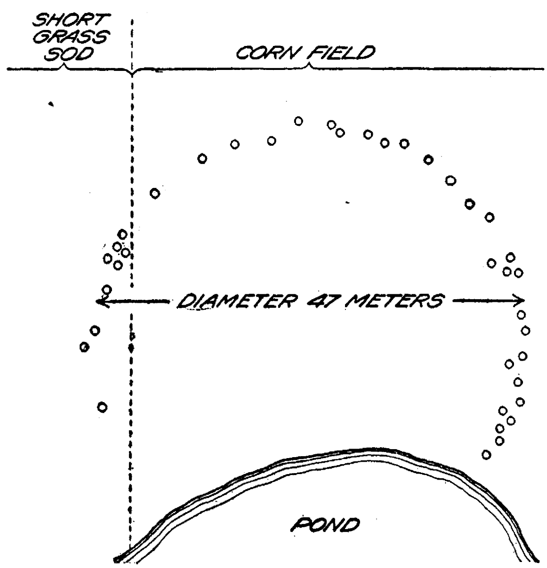

FIG. 10.—This *Agaricus tabularis* ring was partly within a cornfield and partly within the native short-grass sod. At one side the ring had been interrupted by the presence of a pond. The mushrooms in the cornfield showed a taller stipe, a more expanded pileus, and a smooth top, while those in the short grass showed a short stipe and a compact pileus with a roughened top characteristic of *Agaricus tabularis*.

The effect of the dry climate on *Calvatia cyathiformis* is not as marked as on *Agaricus tabularis*. The peridium, which is usually dried rapidly, has a rough tabular appearance. As soon as dry, these scales fall off, exposing the spore area underneath (Pl. 27, A). The same is true of *Calvatia fragilis*. *Calvatia polygonia* produces a heavy, thick, scaly peridium (Pl. 29, A, B), which responds especially to the dry conditions of the atmosphere. If the young puffballs are injured, they break open, forming abnormal fruiting bodies, such as shown in Plate 29, C. These fruiting bodies dry up before mature spores can be produced.

AGE AND RATE OF ADVANCE

Very little data are available on the rate of advance of fairy rings. Hutton (1790) observed this advance during a period of eight or nine years, but gave no data as to rate. Wollaston (1807) measured the annual increase in the rings and found it to be from 8 inches to 2 feet per year.

Thomas (1905) reported on a ring that had been studied especially as to its outward increase for the period from 1896 to 1905. This ring was formed by *Hydnum suaveolens*. In 1896 the ring was nearly complete, but was never complete after that time and only during the years 1901, 1902, and 1905 was there any appreciable increase in outward growth. The average increase of the radius for the period was found to be 23 cm. From this the age of the ring was calculated to be about 45 years.

Ballion (1906) found an increase in the radius of a ring to be 12 cm. during one year, but said the increase was very irregular. The advance was said to be most rapid when the ring was young.

Coulter, Barnes, and Cowles (1911, p. 807) mention a colony of *Hydnum suaveolens* which advanced from 9 to 11 meters in a period of nine years. The age of the colony was estimated to be about 45 years.

Bayliss (1911) found the maximum increase of a ring of *Marasmius oreades* to be 13½ inches per year, and the minimum increase 3 inches. She thought rings might extend for 50 or even 100 years.

Very little data are available on the rate of advance of fairy rings in eastern Colorado. Doubtless it is very unequal, and during dry years little, if any, advance is made. During moist years, such as 1915, the rings make a very decided advance.

The first crop of *Agaricus tabularis* usually occurred near the inner edge of the outer stimulated zone (zone 4, fig. 3). The second crop, which in 1915 occurred two months later, had advanced an additional 8 to 30 cm. (fig. 11).

It is often evident from the old fruiting bodies which have remained in place that the advance is approximately the same for the first as for the second crop. But the rings fruit only during the exceptionally wet years. If it is assumed from these observations that the amount of advance for each crop is approximately 30 cm., we may estimate the age of the rings on the basis of the records of the last 10 years. Four crops have been produced in 10 years, which would correspond to an advance of 120 cm. in this period of time. From observations of the rings during this period these estimates would seem to be approximately correct. On this basis the average yearly advance would be about 12 cm. A ring 60 meters in diameter would be approximately 250 years old. In the southern portion of the area shown on the map (fig. 2) a large number of small or fragmentary rings are roughly arranged in the form of two still larger rings. If these fragments have had a common origin, which seems a correct assumption, the age of these large fragmented rings would be approximately 600 years.

The rate of advance of the *Calvatia cyathiformis* ring is about the same as that of the *Agaricus tabularis* ring during periods especially favorable for growth. The second crop produced in 1915 showed an average advance of from 8 to 30 cm. (fig. 5, 12, and Pl. 25, A, B; 26, A). Judging by the sterile bases of the old fruiting bodies the first crop shows a similar advance over the crop the year before. If we assume this

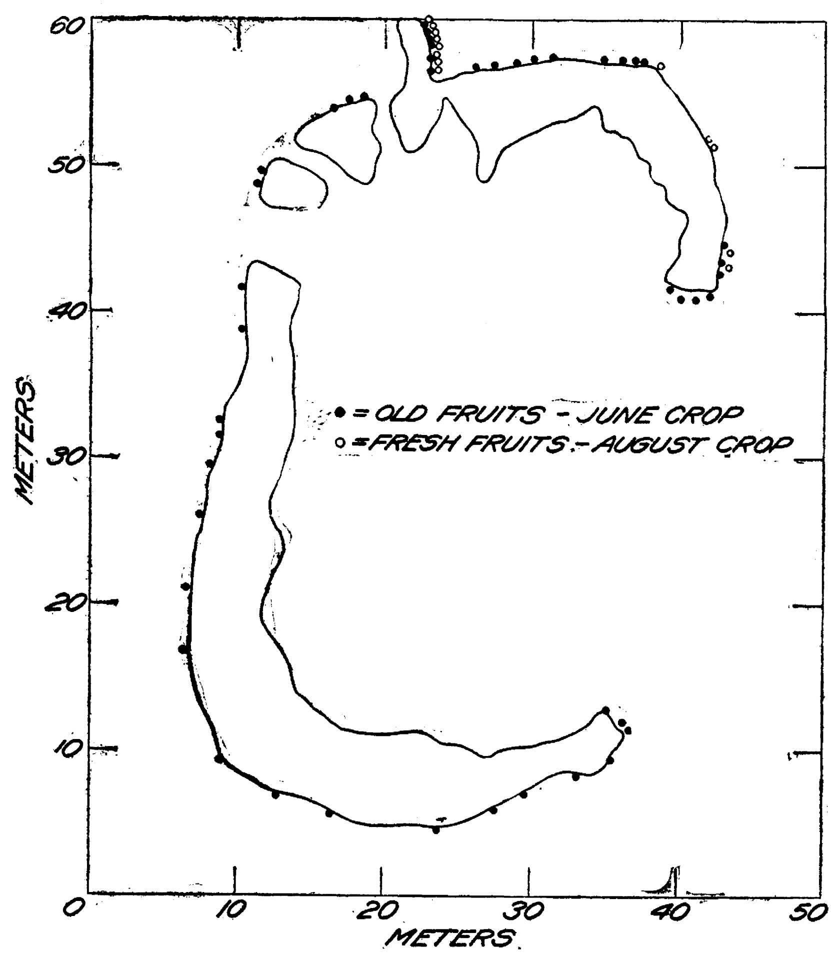

FIG. 11.—A sketch of ring 1 made in August, 1915. The fresh fruiting bodies are shown as circles and the old fruiting bodies as dots. The ring has been interrupted at the upper left-hand side and on the right has apparently come into contact with the second ring which produced a slight extension at the upper part of the figure. The fungus was especially luxuriant in this portion and at this point produced a large number of fruiting bodies in both the first and second crop. The distribution of the fruiting bodies near the interrupted portion of the ring indicates a tendency on the part of these rings to grow around, producing an effect not dissimilar from the effect of tree growth in covering a wound or dead branch.

maximum rate to be 30 cm. per crop, the advance during the 10 years would be eight times this amount, since the fungus fruited only eight times, or a total advance of 240 cm. For the 10 years this would mean an average yearly advance of 24 cm., or about twice as rapid as the estimated yearly advance of *A. tabularis*. The age of the largest rings, which are 200 meters in diameter (Pl. 24, B), would be approximately 420 years.

DISTRIBUTION OF THE MYCELIUM IN THE SOIL

The distribution of the mycelium in the soil can not easily be determined, except for *Agaricus tabularis*. On the high plains the mycelium seldom penetrates deeper than the superficial soil layer, which is dark in color, owing to the presence of organic matter. In most cases the lower

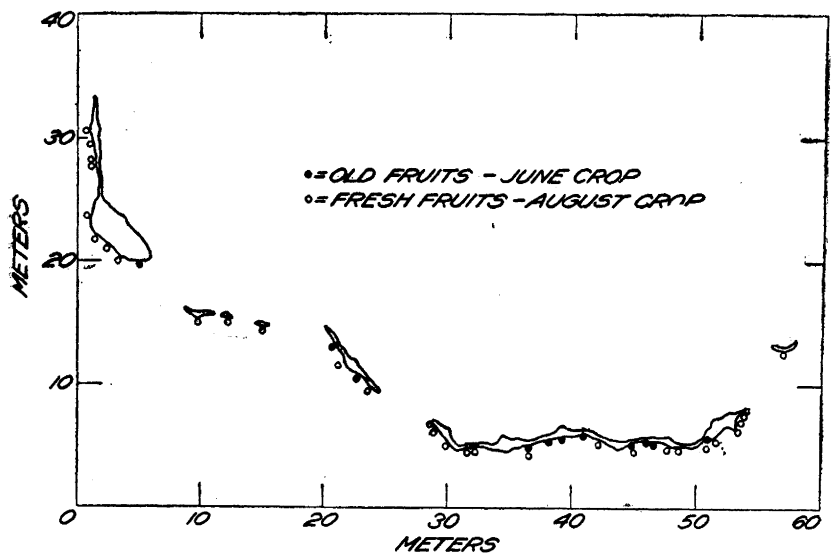

FIG. 12—A detail map of ring 5 shown in the lower left-hand corner of the map. This *Calvatia cyathiformis* ring had produced two crops of puffballs, the first crop being indicated by dots and the second by circles. The zone of influence of the *C. cyathiformis* ring is much narrower than that of the *Agaricus tabularis* ring.

limit of penetration was reached near the inside of the area when the old mycelium had penetrated to a depth of from 5 to 10 cm. below the level of the young mycelium at the front edge of the fungus development.

In no case have the writers found the mycelium nearer to the surface than about 8 cm. This is probably due to the extremely dry condition of the surface soil during a large part of the year. Wollaston (1807), Molliard (1910, fig. 1), and Münch (1914) found the mycelium extending to the surface of the soil. This would be the case where the surface of the soil remained moist for a considerable time. In figures 4 and 13 and in Plates 14, C 15, and 17 the distribution of the mycelium of *Agaricus tabularis* is shown.

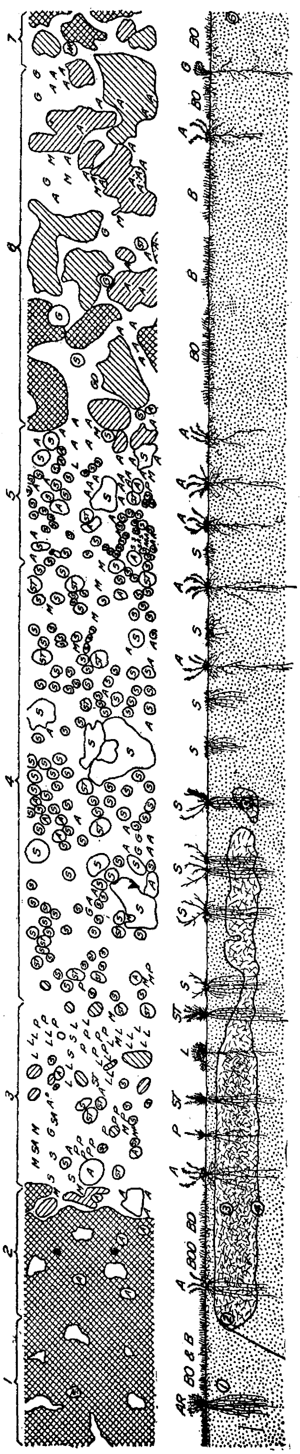

FIG. 13.—A bisect and transect of an *Agaricus tabularis* ring at Akron, Colo., on August 7, 1916. This ring is one possessing unusual vigor and has apparently advanced at a comparatively rapid rate during the last few years. The area of influence of this ring extends to a width of a little over 9 meters. The figures at the top of the transect indicate stages in succession: (1) Is natural short-grass sod; (2) an outer withered zone in which the short grass is dying from drouth; (3) an early weed stage occupied by a few remaining plants of short grass and characterized by the appearance of a few small annuals; (4) short-lived grass stage marked chiefly by Schedonnardus; (5) the perennial stage which shows an abundance of *Artemisia frigida;* (6) the short grass becoming reestablished. The natural short grass is shown at 7. In the bisect below is shown the distribution of the plants mapped in the transect above, and also the distribution of the mycelium of the fungus in the soil. The figures indicate the location from which the samples were taken for ammonia, nitrate, and moisture-content determinations.

EFFECT OF THE MYCELIUM ON SOIL CONDITIONS

The development of the mycelium brings about both chemical and physical changes in the soil.

CHEMICAL CHANGES

The chemical changes consist largely of the reduction of organic matter, brought about by the saprophytic nature of the fungus mycelium, and of the subsequent decay of the mycelium itself, owing to the action of molds or bacteria.

The protein portion of the dead organic matter of the soil is reduced to ammonia, which either unites with other compounds or is changed by bacteria to nitrites and these in turn by other bacteria into nitrates.

There duction of the organic material thus furnishes a quantity of readily available nitrogenous material for the use of the green plants. Since on account of the dry subsoil and small amount of rainfall no leaching takes place in the soils in eastern Colorado, the chances for loss of nitrogen are greatly reduced.

As the mycelium passes on to new soil the old mycelium dies. The death of this mycelium is followed by decay produced by bacteria and molds which again liberates a supply of nitrogenous material for higher plants. The result is an increase in plant growth, the production of more roots in the soil, and consequently an increase in the organic matter contained in the soil.

Wollaston (1807) spoke of the exhaustion of the "pabulum" of the soil necessary for the growth of the fungus, but did not state of what this "pabulum" consisted.

According to Buckman (1870), anything which would kill a patch of grass and thus give the fungus something (organic matter) on which to live would produce a fairy ring.

A special study of the carbon content of the soil in fairy rings was made by Lawes, Gilbert, and Warington (1883). The percentage of carbon (Table V) was found to be uniformly higher outside the ring than either in the ring or within the ring. The determinations in and inside the ring differ only slightly, the smallest amount of carbon being recorded inside the ring.

TABLE V.—*Mean percentages of carbon* [a] *in the fine dry fairy-ring soils, according to Lawes, Gilbert, and Warington (1883)*

Description of ring.	Percentage of carbon.		
	Within the ring.	On the ring.	Outside the ring.
Grove Paddock (May, 1874)	3.06	2.72	3.34
Broadbalk (June, 1877)	2.38	3.36	3.29
Broadbalk (September, 1877)	2.48	2.60	3.12
Park (September, 1877)	2.88	3.21	3.31
Park (April, 1878)	3.12	3.04	3.44
Mean	2.78	2.99	3.30
Carbon "outside" = 100	84.2	90.6	100.00

[a] Carbon determined "by combustion in oxygen."

The percentage of organic carbon in the soil in the different sections of *Agaricus tabularis* rings at Akron, Colo., is presented in Table VI. It is evident from this table that no significant differences are noted in the organic carbon content. The organic carbon content, with one exception, ranges from 2.15 to 3.79 per cent. Difficulties are encountered in determining the carbon content where the soil contains only a small amount of organic matter. It is evident in this case that the errors due to the inclusion of the roots of plants are so great as to obscure to a great extent the effect of the growing mycelium on the organic matter of the soil.

TABLE VI.—*Percentage of organic carbon*[a] *in rings of Agaricus tabularis at Akron, Colo.*

Sample No.	Location.	Ring B.	Ring 2.	Ring 8.	Ring 6.	Ring 7.
1	Outside	2.37	2.76	3.26	2.69	2.97
2	Youngest mycelium	2.58	2.87	2.83	2.93	3.33
3	Dense mycelium	2.15	3.17	3.50	2.91	3.02
4	Below No. 3	2.23	2.89	3.79	2.94	3.05
5	Old dying mycelium	2.23	2.73	2.87	3.23	2.81
6	Inside	2.34	2.45	3.43	2.64	.98

[a] For the determination of organic carbon the writers are indebted to Dr. E. C. Shorey, of the Bureau of Soils. The determinations were made by the moist-combustion method with sulphuric acid and potassium bicromate.

One of the principal effects of the growth of the fungus mycelium in the soil is in changing the nitrate or ammonia content of the soil.

Lawes, Gilbert, and Warington (1883) found more nitrogen outside the ring than either in the ring or inside the ring (Table VII). The same results were obtained for carbon (Table V) and the ratio of carbon to nitrogen was found to range from 11.2 to 11.7. They also determined the nitrates and found here a much greater amount in the ring than either inside or outside (Table VIII). From the results it was concluded that in fairy rings the nitrates of the soil were greatly increased and that the source of the nitrates was the organic matter of the soil.

TABLE VII.—*Mean percentages of nitrogen*[a] *in the fine, dry fairy-ring soils, according to Lawes, Gilbert, and Warington (1883)*

Description of ring.	Percentage of nitrogen.		
	Within the ring.	On the ring.	Outside the ring.
Grove Paddock (May, 1874)	0.262	0.274	0.287
Broadbalk (June, 1877)	.271	.300	.315
Broadbalk (September, 1877)	.226	.244	.274
Park (September, 1877)	.222	.253	.259
Park (April, 1878)	.253	.257	.269
Mean	.247	.266	.281
Nitrogen "outside"=100	87.9	94.7	100.000
Ratio of carbon to nitrogen	11.3	11.2	11.7

[a] Nitrogen determined "by combustion with soda-lime."

Molliard (1910) concluded that the mycelium acted directly on the humus of the soil and that the reduction of the organic matter of the soil gave rise to ammoniacal salts. The amount of ammonia found in different portions of the ring (fig. 1) is shown in Table IX. The greatest amount was found under the dead zone (III) and in the mycelium area under the outer stimulated zone (IV). No significant difference was noted between the inside and the outside of the ring.

TABLE VIII.—*Nitrogen as nitrates per million of dry fine soil, according to Lawes, Gilbert, and Warington (1883)*

Location.	Crum-Frankland method.	Schlösing method.	Location.	Crum-Frankland method.	Schlösing method.
Broadbalk fairy-ring soils, collected June 18, 1887:			Park fairy-ring soils collected Sept. 19, 1877:		
Within the ring.....	0.23	....	Within the ring.....	Trace.	....
On the ring..........	.92	....	On the ring (center)..	.46	....
Just outside the ring.	.43	....	On the ring (outer edge)............	1.21	....
Outside the ring.....	.09	....	Just outside the ring.	Trace.	....
Broadbalk fairy-ring soils, collected Sept. 15, 1877:			Park fairy-ring soils, collected Apr. 25, 1878:		
Within the ring......	1.31	1.03	Within the ring......	.17	....
On the ring..........	8.07	11.46	On the ring (inner side)............	1.21	....
Outside the ring.....	1.10	2.44	On the ring (outer side)............	None.	
			Outside the ring.....	.18	....

TABLE IX.—*Quantity of ammonia (in milligrams) in 100 gm. of dry soil according to Molliard, 1910*

Zone.	Location.	Ammonia taken up by the water.	Ammonia retained by soil.	Total ammonia.
I........	Inside, no mycelium......................	4	33	37
III......	Dead-grass zone, in mycelium............	14	66	80
IV (s)....	Outer stimulated zone (above mycelium area)................................	8	45	53
IV (p)...	Outer stimulated zone (in mycelium area)...	17	56	73
V.......	Outside (normal) no mycelium.............	3	35	38

The determinations of [1] nitrogen in the form of ammonia and nitrates in rings formed by *Agaricus tabularis* in 1915 are given in Table X. The soil samples were taken with a soil tube and consisted of a core of soil extending through the first 6 inches, the first foot, or the second foot of soil. The results in the second foot are less significant than those in the first foot, since less of the mycelium lies in this area. It will be noted as a rule that the ammonia content is higher in the ring than inside, and higher inside the ring than outside. In the case of nitrates the results are not conclusive, although as a rule the nitrates are more abundant in the ring and inside than under the normal sod outside. In 1916, samples of soil were taken in six carefully selected places in a trench dug across a number of different rings formed by *Agaricus tabularis*.

[1] For the determination of nitrates and ammonia the writers are indebted to Mr. R. C. Wright, of the Office of Soil-Bacteriology Investigations, Bureau of Plant Industry. The determinations were made by a modified Ulsch method. Two hundred c. c. of soil extract were treated with one c. c. of concentrated sulphuric acid and five gms. of reduced iron powder, and the reduction was allowed to proceed from 12 to 15 hours. This solution was then made alkaline with magnesium oxid and distilled into standard acid.

The location of these samples is indicated in the case of ring 2 in figure 13. The results are shown in Table XIII. In these determinations the first figure indicates results on the comparatively fresh soil; the second figure is a determinatian made on a duplicate sample which had remained in a dry condition in the laboratory for about seven months. Nitrates were least abundant on the inside of the ring and most abundant in the part occupied by the old dying mycelium. In the area occupied by the young mycelium and just below it, and also in the mass containing the dense portion of the mycelium, the nitrate content was about uniform. Ammonia was least abundant inside the ring, and most abundant in the dense portion of the mycelium. In the case of the new mycelium and the area just below the dense mycelium the ammonia content was about the same. More ammonia was found outside in the native sod than on the inside of the ring. The total nitrogen was determined in duplicate from dried samples. It is evident that the changes in the quantity of nitrates or ammonia recorded in different portions of the soil mass are not accompanied by changes in the total nitrogen content of the soil. In other words, the nitrogen seems only to be changed from one form to another.

TABLE X.—*Quantity (in parts per million) of ammonia and nitrates in Agaricus tabularis rings, Akron, Colo., 1915*

Ring No. and date.	Depth.	Nitrogen in the form of ammonia.			Nitrogen in the form of nitrates.		
		Outside zone No. 5.	Bare zone No. 3.	Inner stimulated zone No. 2.	Outside zone No. 5.	Bare zone No. 2.	Inner stimulated zone No. 2.
	Feet.						
Ring 1, July 13, 1915	1	19	61	24	0	11	8
Do	2	5	21	11	3	8	5
Ring 2, June 16, 1915	1	.....	.....	.....	20	14	38
Do	2	.....	.....	.....	14	12	24
Do	3	.....	.....	.....	20	8	24
Ring 2, July 13, 1915	1	.....	.....	.....	12	14	Tr.
Do	2	.....	.....	.....	6	Tr.	.....
Do	3	.....	.....	.....	Tr.	Tr.	0
Ring 3, July 13, 1915	1	16	48	24	3	11	11
Do	2	11	16	8	3	5	5
Ring 4, Aug. 16, 1915	½	16	59	24	11	11	14
Ring in oats, July 17, 1915	1	16	24	16	0	5	5
Do	2	11	19	11	0	5	3
Ring in wheat field, Aug. 12, 1915	.....	19	53	.....	5	24	.....
Mean	1	17	49	22	7	13	13
Do	2	9	19	10	5	6	9
Do	3	.....	.....	.....	10	4	12

The determinations of nitrogen in the form of ammonia and nitrates in *Calvatia cyathiformis* rings for 1915 are summarized in Table XI. In the case of rings of *C. cyathiformis* more ammonia was found in the outside than on the inside or in the zone which had produced fruits. In the case of nitrates the reverse was found to be the case, the nitrates being somewhat more abundant in the ring than either outside or inside. The determinations from samples taken in 1916 are given in Table XII.

TABLE XI.—*Quantity (in parts per million) of ammonia and nitrates in Calvatia cyathiformis rings, Akron, Colo., 1915*

Ring No. and date.	Depth.	Nitrogen in the form of ammonia.			Nitrogen in the form of nitrates.		
		Outside.	In ring.	Inside.	Outside.	In ring.	Inside.
	Feet.						
Ring 5, June 26, 1915	1	19	21	19	3	0	8
Do	2	11	11	11	3	5	0
Ring 5, July 13, 1915	1	......	......	......	10	8	6
Do	2	......	......	......	Tr.	6	Tr.
Do	3	......	......	......	Tr.	10	Tr.
Ring 5, July 28, 1915	½	13	37	34	8	11	11
Ring 5, Aug. 16, 1915	½	......	......	......	Tr.	Tr.	Tr.
Mean	1	13	29	27	5	5	6
Do	2	11	11	11	2	6	Tr.
Do	3	......	......	......	Tr.	10	Tr.

TABLE XII.—*Quantity (in parts per million) of nitrogen as ammonia and nitrates in Calvatia cyathiformis rings, Akron, Colo., 1916*

	Sample No.	Nitrogen in the form of ammonia.				Nitrogen in the form of nitrates.			
		Y-8.	Y-9.	Y-10.	Average.	Y-8.	Y-9.	Y-10.	Average.
Outside	1	4.3	......	4.3	4.3	7.1	5.7	8.6	7.1
Among new fruiting bodies	2	1.4	2.9	5.7	3.3	2.9	8.6	12.9	8.1
Among old fruiting bodies	3	1.4	.0	2.9	1.4	8.6	7.1	10.0	8.6
Inside	4	2.9	2.9	2.9	2.9	8.6	......	5.7	7.1

Ammonification took place in all samples shown in Table XIV. The greatest increases were recorded in the soil outside the ring. Nitrification was low in this sample. In the young mycelium ammonification and nitrification were almost as rapid as in the natural soil. In the soil with dense mycelium both ammonia and nitrates were relatively high at the beginning of the experiment. Ammonification was rapid, but nitrification very slow during the first 5-day period. At the end of 2 weeks the ammonia had increased even more than during the 5-day period, while the nitrification was very high, much of the ammonia having been transformed. In the old mycelium the ammonia content was very low and nitrate content relatively very high at the beginning of the experiment. After five days and two weeks the nitrate content was still high and the ammonia content relatively low.

TABLE XIII.—*Quantity (in parts per million) of nitrogen as ammonia and nitrates and N^2 in Agaricus tabularis rings, Akron, Colo., 1916*

Sample No.	Location.	Nitrogen in the form of ammonia.					Nitrogen in the form of nitrates.					Total nitrogen as N^2.[a]				
		Ring 6, June 21.	Ring 7, June 26.	Ring B, June 28.	Ring 2, July 13.	Ring 8, July 18.	Ring 6, June 21.	Ring 7, June 26.	Ring B, June 28.	Ring 2, July 13.	Ring 8, July 18.	Ring 6, June 21.	Ring 7, June 26.	Ring B, June 28.	Ring 2, July 13.	Ring 8, July 18.
1	Outside (see fig. 13)	2.9	1.4	4.3	7.9	5.7	8.6	11.4	11.4	10.7	4.3	1,190	840	770	1,050	1,190
1	.....do	5.0	4.0	9.5	7.6	3.8	4.0	5.0	3.8	1.9	.0	1,120	840	700	910	1,050
2	Youngest mycelium	8.6	10.0	12.4	6.4	12.8	14.3	11.4	21.4	6.4	11.4	1,120	1,050	770	1,050	910
2	.....do	17.1	.50	170.	5.0	11.0	.0	.0	.0	4.0	2.0	1,190	910	770	1,050	910
3	Mycelium densest, driest	20.0	17.3	2.9	27.2	75.7	15.7	11.4	12.9	7.9	8.6	910	1,050	700	1,120	1,050
3	.....do	17.0	21.0	21.6	27.0	22.9	2.0	4.0	9.5	11.4	5.7	770	980	840	1,050	1,050
4	Below No. 3	11.4	2.9	4.3	13.0	11.4	10.0	12.9	22.9	11.4	8.6	1,050	840	770	980	1,330
4	.....do	12.0	3.0	1.0	6.0	6.0	8.0	1.0	5.0	6.0	10.0	1,050	770	770	910	1,330
5	Old dying mycelium	11.4	5.7	2.9	6.4	8.6	8.6	34.2	22.9	32.2	22.9	840	840	700	840	910
5	.....do	6.0	17.1	3.0	5.7	14.0	.0	26.0	10.0	30.5	18.0	840	770	700	840	910
6	Inside	2.9	2.9	.0	3.6	2.8	10.0	8.6	1.4	7.2	7.1	1,050	770	700	910	980
6	.....do	5.7	4.0	.0	6.6	9.5	.0	.0	.0	4.0	1.9	980	700	700	910	840

[a] For these determinations the writers are indebted to Mr. H. W. Daudt, of the Bureau of Chemistry. The determinations were made by the Kjeldahl-Gunning-Arnold method.

Under field conditions the growth of the mycelium is accompanied with the production of ammonia. In the older mycelium, on the other hand, the nitrification is rapid and most of the nitrogen is found as nitrates and only a comparatively small amount as ammonia. The nitrification and ammonification determinations are in accord with the determinations made from field samples.

TABLE XIV.—*Ammonification and nitrification (in parts per million) in Agaricus tabularis rings, Akron, Colo., May, 1917* [a]

Sample No.	Location.	Ammonification.			Nitrification.		
		Nitrogen as ammonia originally present in soil.	Nitrogen as ammonia gained after 5 days' incubation with 0.2 per cent of peptone.	Nitrogen as ammonia gained after 2 weeks' incubation with 0.2 per cent of peptone.	Nitrogen as nitrate originally present in soil.	Nitrogen as nitrate gained after 5 days' incubation with 0.2 per cent of peptone.	Nitrogen as nitrate gained after 2 weeks' incubation with 0.2 per cent of peptone.
1	Outside	3.3	59.9	55.9	0.0	5.1	15.3
2	Youngest mycelium	1.5	34.7	39.5	9.0	−1.4	15.8
3	Dense mycelium	21.0	35.2	40.0	21.0	.5	22.8
5	Dying mycelium	1.5	29.0	17.1	34.5	28.5	117.5

[a] These determinations were made by Mr. R. C. Wright, of the Office of Soil Bacteriology, Bureau of Plant Industry.

From the results of previous investigations and from those here presented it is concluded that the progress of the fairy-ring fungus through the soil brings about the following chemical changes. The dead organic matter of the soil is utilized as a food supply for the saprophytic fungus. During the process the carbohydrates are consumed or reduced and parts of the protein material consumed by the fungus and reduced to ammonia. This combines readily to produce ammoniacal salts, or is changed by bacterial action to nitrites which are in turn converted into nitrates. The chief effect, in so far as soil chemistry is concerned, is to change the protein portion of the organic matter of the soil into compounds of nitrogen which are readily available to higher plants.[1]

PHYSICAL CHANGES

The physical differences in the soil in different portions of fairy rings are due to the growth of the fungus and to the effect of the amount of other vegetation developed on the different zones.

Waring in 1837 (Bayliss, 1911, p. 112–116) noticed the effect of the mycelium on the rate of absorption of water by the soil. In Table XV are presented the results of moisture determinations made by Lawes, Gilbert, and Warington (1883). Their results indicate less soil moisture in the ring than either outside or inside. Measurements made by Molliard (1910) showed that the soil was comparatively dry in the zone occupied by the mycelium (Table XVI).

TABLE XV.—*Percentage of water in fresh soil as collected, exclusive of stones, according to Lawes, Gilbert, and Warington (1883, p. 216).*

Location.	Surface soil.	Subsoil.
Grove Paddock fairy-ring soils, May 19, 1874:		
Within ring	16.03	15.68
On ring	12.58	12.30
Outside ring	15.71	16.24
Park fairy-ring soils, Sept. 19, 1877:		
Within ring	22.80	17.04
On ring (center)	19.29	13.13
On ring (outer edge)	18.50	13.23
Just outside ring	23.33	15.03
Park fairy-ring soils, Apr. 25, 1878:		
Within the ring	26.34	19.21
On ring (inside)	26.33	....
On ring (outside)	21.95	19.14
Outside the ring	27.96	19.74

[1] While the details of the process of reduction of the proteid portion of the organic matter have formed no part of these studies, it is interesting to call attention here to the probability that some of the intermediate products, such as amino acids, are utilized directly not only by the fungi but by the higher plants. See Schreiner and Shorey (1910), Schreiner and Skinner (1912), Schreiner and Lathrop (1912), Schreiner (1913), and the review of this subject, with citations of the earlier literature in Lathrop (1917).

TABLE XVI.—*Soil-moisture content of soils in different portions of a fairy ring, according to Molliard, 1910*

Zone.	Zone No.	Percentage of soil moisture.
Dead-grass zone, in mycelium	III	5
Outer stimulated zone, in mycelium	IV (p)	7
Outer stimulated zone, not in mycelium	IV (s)	21
Inside, no mycelium	I	21
Outside, no mycelium	V	21

Bayliss (1911) found soils which contained mycelium difficult to wet, and mentioned a case where a rain which moistened the soil to a depth of 4 inches did not even penetrate the surface in the mycelium area.

The conditions of moisture in the rings formed by *Agaricus tabularis* at Akron, Colo., in 1914, 1915, and 1916 are indicated in Tables XVII, XVIII, and XX. It will be seen from these tables that the soil in the ring is usually very dry in the middle and late summer. During the spring the soil in the ring differs but little from that outside or inside the ring, provided the previous season was not too dry and a sufficient rainfall had occurred during the winter or early spring to wet the whole soil mass.

TABLE XVII.—*Moisture content above or below the wilting coefficient in two Agaricus tabularis rings on May 16, 1914, Akron, Colo.*

Ring A.			Ring B.		
Depth.	Percentage of moisture.		Depth.	Percentage of moisture.	
	Outside.	In bare area, zone 3.		Outside.	In bare area, zone 3.
Inches.			*Inches.*		
1 to 3	+17.8	+18.6	1 to 3	+23.3	+20.1
3 to 6	+17.3	+13.7	3 to 6	+16.4	+ 2.0
6 to 12	+ 4.4	− 3.2	6 to 12	+13.8	− 3.2
12 to 18	+10.8	− .5	12 to 18	+11.5	+ 6.9
18 to 24	+ 9.1	.0	18 to 24	+13.0	+ 7.6

The difference in soil moisture may be due to several different causes. In the first place, if the soil is uniformly moist, the stimulated areas in the ring (zones 2 and 4, fig. 3) would be the first to become dry as a result of the stimulation of growth in these areas, since this increase in growth of grasses and other plants dries out the soil rapidly. When once the soil is dry, the mass of fungus filaments which permeate every particle of the soil in zones 3 and 4 in the case of the rings of the *Agaricus tabularis* (Pl. 14, B) will not permit the penetration of water into these soils. In Table XVII the moisture content above and below the wilting coefficient is shown for two *A. tabularis* rings in May, 1915. These samples were taken in 3-inch sections. No differences were noted in the first 3 inches. In the second 3 inches the water content in zone 3 (fig. 3) was greatly reduced in the case of ring B, while in the second 6 inches no water at all was available in the ring, though the soil outside of the ring still contained available moisture. In Table XVIII the moisture content above or below the wilting point in three rings of *A. tabularis* on three different dates in 1915 is shown. While there was only a small amount of available water outside on June 16, there was no available water in the ring. On June 26 a similar condition obtained in the ring, while by July 13 the water content both inside and outside the ring had been reduced to below the wilting point. These differences are not so marked in the second foot. The year 1916 was a dry year and the fungi did not fruit. In figure 13 is shown a bisect in which the place of taking samples is shown. Samples take from four different Agaricus rings in 1916 are shown in Table XIX. In all cases the water content was low, the vegetation being in a dormant condition except outside the ring. During a period of heavy rain the samples at 2, 3, and 4 feet would remain dry, while others would readily become moist.

TABLE XVIII.—*Moisture content above or below the wilting coefficient in three Agaricus tabularis rings in 1915, Akron, Colo.*

Depth.	Ring No.	June 16.			June 26.			July 13.		
		Outside, zone 5.	Bare area, zone 3.	Inner stimulated, zone 2.	Outside, zone 5.	Bare area, zone 3.	Inner stimulated, zone 2.	Outside, zone 5.	Bare area, zone 3.	Inner stimulated, zone 2.
First foot....	1	+ 9.3	+0.2	+ 6.7	+1.8	−1.7	+1.0	+0.1	−2.3	−2.9
Do......	2	+11.4	−2.1	+10.4	+3.0	−1.8	−1.4	−2.1	−4.2	−2.8
Do......	3	+ 6.7	−2.9	+ .1	+2.5	−3.5	−2.4	−2.5	−2.7	−3.9
Mean..	......	+ 9.1	−1.6	+ 5.7	+2.4	−2.3	− .9	−1.5	−3.1	−3.2
Second foot..	1	+10.4	+6.8	+ 5.8	+7.8	+1.4	+2.8	+4.4	+1.6	−3.7
Do......	2	+ 9.2	+7.4	+ 9.0	+8.6	+2.0	+1.8	+3.5	−2.3	+2.7
Do......	3	+ 8.5	−3.0	+ 5.4	+6.1	−2.8	+ .4	+2.5	−1.4	−1.4
Mean..	......	+ 9.4	+3.7	+ 6.7	+7.5	+ .2	+1.7	+3.5	− .7	−2.4
Third foot...	1	+ 9.5	+4.8	+ 5.9	+7.4	+2.9	+3.6	+4.2	+1.6	−2.1
Do......	2	+ 9.2	+3.5	− .7	+8.2	+2.9	+ .6	+6.1	+ .6	+3.5
Do......	3	+ 9.5	−4.1	+ 4.3	+8.6	−2.3	+4.0	+6.5	+ .3	+1.3
Mean..	......	+ 9.4	+1.4	+ 3.2	+8.1	+1.2	+2.7	+5.6	+ .8	+ .9

In the case of rings of *Calvatia cyathiformis* the effect of stimulated growth is the same as in the case of *Agaricus tabularis*. The mycelium does not become dense enough to interfere with water penetration, and after each rain the soil is again moistened. Table XX indicates clearly the effect of the stimulated growth of vegetation on the reduction of soil moisture. The soil in the ring is first to be dried below the wilting point.

TABLE XIX.—*Soil-moisture content above or below the wilting coefficient in Agaricus tabularis rings in 1916, Akron, Colo.*

Sample No. and location.	Ring 2, June 12.	Ring 6, June 21.	Ring 7, June 26.	Ring B, June 28.	Average.
1, outside (see fig. 13)	−0.2	+0.3	+3.2	+4.8	+2.0
2, youngest mycelium	+ .5	−2.3	−4.1	−1.8	−1.9
3, mycelium densest driest	−1.7	.0	−2.5	−2.3	− .6
4, below No. 3	−1.1	−1.5	−1.7	− .6	−1.2
5, old dying mycelium	− .6	−2.2	−1.4	−2.5	−1.7
6, inside	−2.5	− .8	−4.1	−2.8	−2.6

TABLE XX.—*Moisture content above or below the wilting coefficient in a Calvatia cyathiformis ring in 1915, Akron, Colo.*

Ring No.	Depth of soil.	June 26.			July 13.		
		Outside, zone 5.	In stimulated area 2.	Inside, zone 1.	Outside, zone 5.	In stimulated area 2.	Inside, zone 1.
	Feet.						
Ring 5	1	+2.2	−1.3	+0.5	−0.8	−2.6	−1.2
Do	2	+6.4	+1.0	+5.5	+3.3	−2.9	+ .7
Do	3	+6.8	+1.7	+3.5	+4.1	−2.8	+2.7

For the purpose of studying the penetration of water both into the mycelium infected soil and into the natural sod outside, a strip about 9 meters long was selected on the edge of a ring of *Agaricus tabularis* where the zones were well defined. Holes were made 6 inches deep with a soil tube. They were made in rows 1 meter apart, consisting of three holes each. One row was outside in the natural sod (fig. 3, zone 5), the next row at the border between the withered (fig. 3, zone 4) and bare areas (fig. 3, zone 3), and the third row in the bare area. Two-liter flasks of water were then inverted into the holes to determine the rate of penetration (Pl. 23,A). The results are given in Table XXI.

In both records the number of cubic centimeters of water that penetrated into the soils was much greater in the natural sod outside the ring and least at the border line between the withered and bare areas where the mycelium was most dense. The individual records vary considerably. This is probably largely due to the varying density of the mycelium in the soil and to differences in the dryness of the soil. In the first measurements the penetration in the outside was three times as rapid outside as in the withered zone and twice as rapid as in the bare zone. The difference is a little less marked in the second experiment due partly to the fact that part of the soil had already been moistened by the first irrigation. After heavy rain the water stands on the soil over these rings of *Agaricus tabularis*, while on the adjacent land it soon penetrates and disappears. Several hours after a rain the surface soil will be muddy just above the dry hypha-filled portion. When these hyphae are dry, water is turned off just as from a dense mass of nonabsorbent cotton. The figures in Table XXI do not fully convey the difference in moisture penetration since under field conditions the moisture is free to run off on adjacent land and the relative amount of water which penetrates the soils of the *Agaricus tabularis* fairy ring is consequently smaller than would be indicated by the table. The effect of rain in moistening the soil of an *Agaricus tabularis* ring is shown in Plate 15. The mycelium-filled soil shows light in the soil trench. The water penetrated both in front of and back under the edge of the mycelium-filled soil without wetting the latter. The moist soil appears dark in the soil trench.

TABLE XXI.—*Rate of penetration (in cubic centimeters per hour) of water into the soil of an Agaricus tabularis ring, Akron, Colo., 1915*

Record No.	Outside.	At the border of withered and bare areas.	In the bare or nearly bare area.
First record, begun June 12	12.5	20.9	22.7
	30.8	12.3	20.9
	41.7	6.4	9.3
	83.4	41.7	22.7
	41.7	20.9	22.7
	41.7	6.4	83.4
	83.4	7.6	60.0
	83.4	27.8	22.7
	83.4	10.8	22.7
Average	55.7	17.2	31.9
Second record, same place, begun June 26	87.0	69.0	46.5
	46.5	44.5	69.0
	87.0	44.5	69.0
	105.0	69.0	46.5
	74.0	87.0	46.5
	87.0	27.4	69.0
	105.0	29.0	105.0
	95.3	69.0	27.4
	105.0	46.5	29.9
Average	88.0	54.0	56.5

EFFECT OF FAIRY RINGS ON VEGETATION

RINGS OF AGARICUS TABULARIS

The first effect noted by the penetration of the filaments of this fungus into the soil occupied by short-grass vegetation is the slight stimulation of all the native plants. The stimulation (fig. 3, zone 4) is noted in the deeper color of the short grasses and in the greater and more rapid growth of the annuals (*Plantago purshii, Festuca octoflora, Hedeoma nana,* etc.)

and the perennial plants such as *Gutierrezia sarothrae* and *Artemisia frigida*, all of which grow in the native sod. The fruiting bodies of the fungus occur in this stimulated zone. The soil in the area just inside zone 3 (fig. 3) is permeated with filaments of the fungus from a depth of about 8 cm. to a depth of something over 30 cm. During years of normal or subnormal rainfall the soil of this zone is dry, and since water does not penetrate this soil, this zone is marked by dead or dying plants, or by the absence of a plant cover of any kind. Inside this bare zone, where the mycelium has died and partly disappeared and where moisture can penetrate more freely, the vegetation which is now composed largely of ruderals (fig. 13), is as luxuriant as is permitted by the soil-moisture supply and the increase in available nitrogenous material. The vegetation on the inside of the ring (zone 1) does not differ in composition and appearance from that outside (zone 5), although it has been destroyed and reestablished.

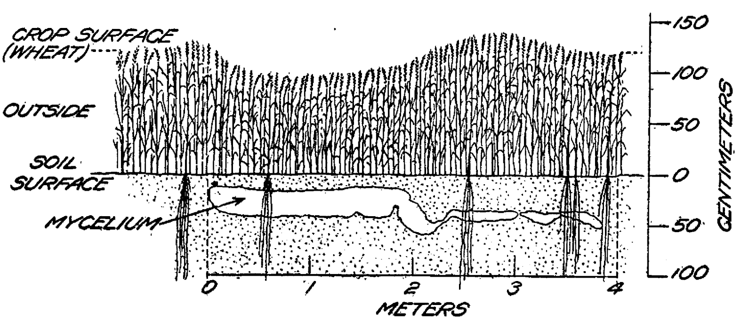

FIG. 14.—A bisect of a ring of *Agaricus tabularis* in a wheat field in 1915, a year of ample moisture supply.

The effect of the fairy ring caused by *Agaricus tabularis* on the native vegetation varies greatly with the moisture supply. The appearance of the ring is entirely different during a dry year (Pl. 16) and during a wet year (Pl. 19), and no description can be given which will apply at all times. The zones of greatest potential stimulation of plant growth due to available nitrogenous material may be brown and dry, owing to the lack of available soil moisture. The dead zone is only an expression of the extreme drouth produced by the combination of dry weather and unfavorable soil conditions. If rain is continuous and well distributed, the vegetation does not die, and a ring in which the bare zone has all but disappeared is the result. This condition was produced artificially in 1916 (Pl. 23, B). But since such a combination of favorable conditions seldom occurs in eastern Colorado the bare zone is well marked during normal years and can be distinguished even during wet years. The bare zone originates in the outer stimulated zone. During summer or late fall, or during dry years, this is changed to a withered condition, and if drouth is prolonged, to a bare condition due to the death of the grasses.

By gradual extension the mycelium develops another stimulated zone outside, and this in turn withers. In this way the dead zone is gradually increased on the outer edge. As the mycelium under this area becomes older it gradually dies out. Water penetration then becomes more normal and the ample supply of available nitrogenous material produces the inner stimulated zone.

The effect of rings of this type on cultivated plants is about the same as on the native plant cover. During a wet year the relative stimulation and depression of growth of the different areas is shown in the bisect (fig. 14; see also Pl. 21). The wheat just beyond the mass of mycelium showed a slight stimulation as compared with that entirely outside the ring. Over the area of dense mycelium the plants ripened prematurely and did not produce as much straw as in the normal crop. The grain production was very low. Back of the dense area of mycelium the fungus filaments were evident only at greater depths in the soil, and here the greatest stimulation of the wheat crop occurred. The results of croppings made at this time are shown in Table XXII.

TABLE XXII.—*Yield of wheat per square meter in a ring of Agaricus tabularis*

Item.	Inside (1).	Bare zone (3).	Outside (5).	Ratio 3:5.
During a wet year, Akron, Colo., Aug. 12, 1915:				
Wheat ring—				
Number of heads	....	108	190	57
Height ... cm.	....	93	210	44
Total dry matter ... gm.	....	401	500	80
Grain ... gm.	....	63	137	46
During a dry year, Akron, Colo., July 6, 1916:				
Wheat ring 8—				
Total dry matter ... gm.	91	0	108	....
Wheat ring 9—				
Number of heads	150	30	277	12
Height ... cm.	50	30	57	53
Total dry matter ... gm.	156	34	260	13
Wheat ring 10—				
Number of heads	54	0	160	....
Height ... cm.	35	0	50	....
Total dry matter ... gm.	57	0	132	....

In the same table the effect of the fairy ring on a wheat crop during a dry year is shown (Pl. 22). The zone just above the densest area of mycelium (bare zone 3) was then practically free of plant growth. The results in the table indicate clearly the harmful effect of this fungus on the crop during normal or dry seasons. Only in the case of ring 9 was any wheat produced in the bare zone, and the yield there was partly due to the width of the zone (only about 1 meter' and to the slight extension of the cropping into the adjacent zones.

In an oat field in 1915 a similar effect was noted but instead of a depressed growth over the dense mycelium area, the moisture supply had been sufficient to mature the crop on most of this zone. Along the line of fungus fruiting bodies the oat plants were small and weak. The relative height of the oat plants in different portions of the ring is given in Table XXIII.

TABLE XXIII.—*Height of oat plants in different zone of an Agaricus tabularis ring Akron, Colo., July 12, 1915.*

Zone.	Zone No.	Height of plants.
		Cm.
Inside	1	77
Inner stimulated zone	2	112
Fruiting zone	4	60
Outside	5	76

It is evident that in this case drouth was not operating to the detriment of the oat plants in such a wide portion of the area, and the usual depression of growth over the dead zone was not evident except in the immediate vicinity of the fungus fruits. The land had been plowed in the spring, and the heavy and continuous rains had maintained even the mycelium-impregnated soil in a moist condition.

RINGS OF CALVATIA CYATHIFORMIS

In figures 5 and 6 the principal zones found in rings formed by this fungus are sketched. The only effect produced on the vegetation by this fungus is to stimulate the growth on the area just inside the fruiting zone. The short grasses are not injured in these rings, and the weedy annuals do not enter. *Festuca octoflora, Plantago purshii, Hedeoma hispida*, and the short grasses usually grow luxuriantly in this stimulated zone. Their growth is more rapid, and the plants darker green in color. The stimulated zone in these rings does not differ essentially as to vegetation from the outer stimulated zone of the ring of *Agaricus tabularis*; and since the perennial vegetation is not killed, the bare zone does not exist, nor is the inner stimulated zone (or weed zone) of the Agaricus ring represented in the Calvatia ring. The position of the stimulated zone in Calvatia rings is within the circle of fruits instead of outside of it, as in the case of the outer stimulated zone 4 in Agaricus rings.

The vegetation inside does not differ from that outside, excepting following years of more than normal moisture supply, when the short grass cover just inside becomes more dense than outside, due to better growth in the stimulated zone (Pl. 27, B).

The effect of *Calvatia cyathiformis* on the cultivated crop is similar to that on the native. During dry years, such as 1916, no effect could be noted. It is evident from the remapping (fig. 8) of the area shown in figure 2 that only rings formed by *Agaricus tabularis* could be found in the wheat field during 1916. These were noticeable because of the depression of the growth of the wheat. Those formed by *C. cyathiformis* could not be distinguished, since they had produced no effect on the crop.

OTHER FUNGUS RINGS

Agaricus campestris, *Calvatia polygonia*, *C. fragilis*, *Catastoma subterraneum* (Pk.) Morg., *Marasmius oreades*, and *Tricholoma melaleuca* do not differ markedly from *C. cyathiformis* in their effect on the vegetation. *Lepiota morgani* occurred in a sandy soil in bunch-grass vegetation (Shantz, 1911, p. 54). No effect was noted on the native cover, although a great number of fruits had been produced.

GRAZING AND CULTIVATION

An especially interesting effect is seen in areas which are grazed. The grass in the stimulated zone appears to be more palatable than the less luxuriant grass in the adjacent sod and this zone is therefore often easily distinguished by the closely cropped grass.

Rings formed by *Calvatia cyathiformis* have not been found fruiting in cultivated fields. *C. polygonia* continues to fruit after land is cultivated, several rings having persisted in fields which have been under cultivation for a period of five years. *Agaricus tabularis* produces rings which seem to persist without injury under cultivation. The ring shown in the wheat field (Pl. 14, C; 21, A) was on land which has been under continuous cultivation for the past seven years. These rings often fruit as well as in cultivated fields as in the native soil.

CAUSE OF THE STIMULATED GROWTH

Practically every investigator of fairy rings has noted a stimulated growth of the natural vegetation on fairy rings. This stimulation was attributed to the decay of the fungus fruits or mycelium by Wollaston (1807), Way (1847), Westerhoff in 1859 (*in* Ritzema Bos, 1901), Berkeley (1860), Jorden (1862), Gilbert (1875), Van Tieghem (1884, p. 1044–1045), Olivier (1891), Stahl (1900), Ritzema Bos (1901), Beille (1904, p. 381), and Massart (1910). The principal constituents which contributed to this stimulation were potash, phosphated alkali, magnesia, and sulphate of lime, according to Way (1847), and nitrogenous and mineral manuring according to Gilbert (1875). Westerhoff in 1859 (*in* Ritzema Bos, 1901) actually produced the stimulated growth of the vegetation by scattering over the surface mushrooms cut up into small pieces. Jorden (1862) attributed the stimulation to the fertilizing effect of the ammonia which the fungus absorbed from the atmosphere. Lawes, Gilbert, and Warington (1883), and Ballion (1906), attributed the stimulation to the decay of fungus fruiting bodies and filaments and to the nitrates and residual products formed by the action of the mycelium on the organic matter of the soil. Molliard (1910) stated that the mycelium acted directly on the organic matter of the soil and produced ammoniacal salts which cause the stimulation of the grass the following season.

Bayliss (1911) attributes the stimulation to the better nitrogenous nutrition due to the action of proteolytic enzyms on the dead roots. Münch (1914) stated that rings which produced no mushrooms showed the same stimulation and that the stimulation could therefore not be entirely due to decaying fruiting bodies.

The mushrooms produced in eastern Colorado seldom decay in place. *Marasmius oreades* and even the species of Agaricus dry up in place and are often blown away. The spore masses of the puffballs are blown away, and the sterile bases remain in place for a year or more until loosened and blown away. Many of the fairy rings fruit only every few years, but are distinctly marked each year by the stimulated growth of the grasses and other plants. Although the fruiting bodies would stimulate the growth of plants where they decay, the conditions in eastern Colorado are such as to minimize their effect.

As already pointed out, the growth of the mycelium produces profound changes in the organic matter of the soil, liberating ammonia, which is again built up into nitrates or may form ammoniacal salts, both of which greatly stimulate the vegetation. The principal stimulation is probably due to these changes. Some indication of the effect of the decay of the mycelium on the stimulated growth may be obtained by a comparison of the rings formed by *Agaricus tabularis* and those formed by other fungi. In the case of *A. tabularis* the ring is very broad, the stimulated zone often extending back 2 to 5 meters or more behind the fruiting zone. In the Calvatia, Marasmius, or Catastoma rings, where only a small amount of mycelium is developed and where it is comparatively difficult to distinguish the threads in the soil, the stimulated zone is always narrow, seldom extending more than a meter behind the fruiting zone. In this case the stimulated area is the area in which the fungus filaments are reducing the organic matter of the soil while in the ring of *Agaricus tabularis* the larger inner stimulated zone is due largely to the decay of the mycelium. A comparison of the amount of ammonia and nitrates in the Calvatia and Agaricus ring shows that the ammonia is comparatively more abundant in the area occupied by the active mycelium and that nitrates are comparatively more abundant in the area of dying mycelium. This suggests that the fungus mycelium reduces the protein of the organic matter rapidly to the end product ammonia but that during decay of the mycelium, which is accomplished by bacteria, and which probably takes place slowly, this end product is rapidly built up into nitrates. It would seem therefore that the greatest stimulation of vegetation would be found in the case of the fungus which had the greatest mass of mycelium. This is undoubtedly true, for in the case of *Calvatia cyathiformis*, where only a small amount of mycelium is developed the stimulated area consists of only a narrow zone near the edge of the ring, while in *A. tabularis* the zone extends far back toward the center of the ring.

From our results it seems likely that the greater amount of stimulation noted on the native sod and cultivated crop is due to the reduction of the nitrogenous organic matter to available nitrates and salts of ammonia, and to the subsequent decay of the fungus filaments which produce the same compounds. A stimulation of vegetation exactly similar to that in the fairy rings was produced artificially at Akron, Colo., by placing ammonium nitrate in shallow holes in the soil and by scattering it over the surface of the soil during the rainy period.

The investigations thus far conducted indicate that the stimulation of the grasses and other vegetation is due principally to the presence in the soil of nitrates and salts of ammonia which are derived from (1) the reduction of the organic matter of the soil; (2) the decay of the fungus fruits; and (3) the decay of the mycelium.

TABLE XXIV.—*Effect of fairy rings on the chlorophyll content of plants, Akron, Colo., 1915.*[a]

RINGS OF CALVATIA CYATHIFORMIS, JUNE 28

Plant.	Percentage of alcoholic extracts of crude chlorophyll.		
	Outside.	In stimulated zone.	Inside.
	Per cent.	*Per cent.*	*Per cent.*
Bouteloua gracilis	100	340	125
Plantago purshii	100	280	120
Bouteloua gracilis	100	175	127
Plantago purshii	100	110	105
Mean	100	226	119

RINGS OF AGARICUS TABULARIS, JUNE 18

Plant.	Outside.	In stimulated zone.	Inside.
Gutierrezia sarothrae	100	110	90
Artemisia frigida	100	200	200
Malvastrum coccineum	100	225	300
Festuca octoflora	100	200	90
Hedeoma nana	100	200	135
Plantago Purshii	100	265	135
Bulbilis dactyloides	100	260	255
Mean	100	209	172

[a] The chlorophyll was extracted from equal areas of leaf lamina by cold 90 per cent methyl alcohol. The extract was made in the dark. Colorimetric determination was made on the crude extract, the values outside being taken as 100.

CHLOROPHYLL CONTENT

One of the most characteristic features of fairy rings is the deep-green color of the vegetation in the stimulated zones. This effect was noted by many investigators, but no quantitative determinations of chlorophyll content have been made. The writers have determined by colorimetric methods the relative density of the crude chlorophyll. Extracts were made in the dark with cold 90 per cent methyl alcohol. The results indicated in Table XXIV show that the chlorophyll content is about twice as great in the stimulated zone as outside. The results are quite uniform for the different plants and also for the Agaricus and Calvatia rings. Similar measurements of the chlorophyll content in oat fields showed the amount in the stimulated zone to be twice as great as normal. The cause of the increase in vigor and chlorophyll content seems to be amply explained on the basis of the available supply of nitrates and salts of ammonia.

CAUSE OF THE DEATH OF THE VEGETATION

The death of the vegetation noted by many investigators has been attributed to a number of different causes. The fungus filaments were thought to absorb all nutrient material from the soil and thus cause the death of the grasses, etc. This view was held by Wollaston (1807), Van Tieghem (1884, p. 1044–1045), Olivier (1891), and Beille (1904, p. 381).

Berkeley (1860, p. 41) attributed the death of the grasses to the effect of the death of the spawn of the fungus, while Jorden (1862) attributed the death of grasses to the entangling action of the filaments and their strong "effluvia."

The cause of the death of the grasses was attributed to parasitism on the part of the fungus by Ballion (1906) and Bayliss (1911), the latter stating that the roots were directly attacked by the fungus filaments and killed by toxic excretion.

The impenetrability of the soil to moisture, or the dry condition of the soil, was believed by Ritzema Bos (1901) and Molliard (1910) to be the chief cause of death of the grass. The latter attributed part of the harmful effect to the high content of ammoniacal salts.

In the investigations of the writers the death of the vegetation noted in rings formed by *Agaricus tabularis* was always accomplished by lack of available soil moisture. No harmful effect could be noted on the vegetation as long as the soil contained available water. During years that were uniformly wet throughout the growing season the vegetation was not noticeably damaged, while during dry years or periods of drouth the plant cover would be partly or entirely destroyed just above the dense mycelium. As stated elsewhere, the penetration of water into the mass of soil filled with mycelium is very slow if the soil is once dried. The stimulation of growth hastens the drying out of this soil mass; and, when once dry, it remains dry even through heavy and continued rain. During ordinary years, when the moisture supply was sufficient on the natural sod, drouth was severe over the mycelium-impregnated soil.

If parasitism or toxic secretion were the cause of the death of grasses in this area, the vegetation would be attacked while still growing and while sufficient moisture remained in the soil to maintain the fungus and the grass roots in active condition. In order to test the effect of the mycelium on the native vegetation, the following experiment was conducted during the dry season in 1916. A strip about 6 meters long and 3 meters wide was selected on the edge of a ring of *Agaricus tabularis* where the zones were well defined. This strip extended 1 meter out from the border line between the withered zone (4) and the bare zone (3), and 2 meters inside of this line over the inner stimulated zone (2), and into the inside (1). The water was poured on slowly to prevent run-off and to give all parts of the plot approximately the same amount. The watering here was begun on June 12 and continued during the next four days. An equivalent of 2 inches of rainfall was added to the plot. On June 28 the plot, in contrast to the dry sod, stood out sharply because of the tall growth and fresh green color of the vegetation. A trench cut across the area just after the irrigation (Pl. 24, A) showed the soil to be only slightly moistened under the bare zone (3) and outer stimulated zone (4), but much moister under the inner stimulated zone (2). The upper 3 or 4 inches in the bare and outer stimulated zone were quite moist. By July 24 the grass, which had grown up rapidly on the bare zone, had again become dormant, owing to drouth. The plot was accordingly irrigated a second time with an equivalent of 3 inches of rainfall. By August 14 (Pl. 23, B) *Grindelia squarrosa, Psoralea tenniflora, Malvastrum coccineum, Gutierrezia sarothrae*, and *Artemisia frigida* were all much more vigorous here than in the natural sod. Culms of grama grass were 10 to 12 inches high and abundant on the plot, but out in the normal sod, where the grass had fruited but rarely, they were only 4 to 6 inches high. The few remaining plants in this bare area had revived and spread until it required close examination to distinguish the various zones, although the grass was denser and somewhat taller in the outer stimulated zone (4) just outside of the bare zone (3).

It seems evident from the behavior of the vegetation under irrigation that the fungus does not directly attack the grasses, nor does it injure them by producing harmful decomposition products. It does, however, bring about a condition of almost certain drouth, under which even the grama and buffalo grasses of the Great Plains die.

ERADICATION OF FAIRY RINGS

Fairy rings cause bare paths and spots, ununiform growth, and unequal color in lawns. Since the value of a lawn is entirely dependent upon the uniform appearance of the turf, the presence of even a small area influenced by fairy rings destroys the effect of the whole. Usually these dead areas are reseeded, but no good effect can be secured in this way, since the fungus mycelium moves on into new grass, and the following year the appearance is as bad as before. In meadows the effect is similar to that on lawns, while in cultivated fields the rings may cause a total loss of the crop over the areas occupied by the ring. In some areas these rings are very numerous. It is estimated that they influence between 0.5 to 1 per cent of the area shown in the map (fig. 1). Even a 1 per cent reduction in gross yield is important when deducted from the net profit. Although there are areas where no fairy rings occur, other areas are badly infested with them. Often areas are found where the rings are more abundant than shown on the map.

In experimental plots the presence of fairy rings is a serious obstacle. A large ring of *Agaricus tabularis* may reduce the yield of a one-tenth acre plot to 50 per cent. Under a most favorable set of climatic conditions it may greatly increase the yield. It is therefore impossible to rely on results from plots occupied by fairy rings. Many of the inequalities of experimental plots are due to this cause, and the eradication of rings on such plots is as important as the experiments which are conducted on the plots.

Persoon (1819, p. 4) observed that if a ring was dug up successively for one or two years the same species reappeared eventually, but it was solitary and scattered.

Sorauer (1886 p. 270–272) stated that repeated digging up of the soil at the periphery of the ring would dry and kill the fungus.

McAlpine (1898) recommended soaking the ground thoroughly with sulphate of copper (or Bordeaux mixture), sulphate of iron 10 per cent, and strong lime water to kill the fungus.

Ritzema Bos (1901) stated that the rings could be destroyed by digging them up in dry, hot weather and exposing the soil to sunshine.

The principal methods suggested for the destruction of fairy rings have been the application of sulphates of copper and iron or repeated stirring of the soil, especially during dry periods. The latter method would be best when applied to experimental plots, since it would not introduce into the soil chemical substances which might possibly have a subsequent effect on crop production. Where the method of digging up the soil is not practicable, the application of fungicides, such as Bordeaux mixture, to the soil immediately over and a little in advance of the rings should be effective.

SUCCESSIONS INDUCED BY FAIRY RINGS

None of the previous investigators made a study of the revegetation following the destruction of the vegetation in the fairy ring. Tulasne and Tulasne (1851, p. 157) mentioned the fact that the production of weeds is due to the digging up of the soil by truffle hunters. Ballion (1906) noted the fact that at the first rains in the fall the perennials on the denuded zone, like "*ravenelles*" (wallflower) and "*oseille*" (sorrel), began to grow again and annuals sprang up from seeds fallen on the bare ground. None of the other investigators mentioned the effect on revegetation.

The effect of *Calvatia cyathiformis* and the other fungi which do not produce a bare zone is the temporary stimulation of the natural vegetation. This influence seldom covers a zone more than a meter wide. The effect on the short grasses is to thicken the sod during years of ample moisture supply (Pl. 27, B.).

Agaricus tabularis kills out the vegetation and initiates a succession (fig. 15) not essentially different from that occurring on abandoned tilled land (Shantz, 1911) or on abandoned roads (Shantz, 1917). The original vegetation is often entirely killed. On the inner part of the area of bare ground weeds develop to form the first stage in the succession. In this area, which lies above the dense mycelium, the weeds which start growth during the spring rainy season are usually killed by drouth while still very small.[1] This area of stunted annuals (fig. 15) constitutes the first or early-weed stage in the succession and consists chiefly of the annuals which are ordinarily abundant in the native sod, such as *Plantago purshii* R. and S., *Festuca octoflora* Walt., *Hedeoma hispida* Pursh., *Lepidium ramosissimum* A. Nels.

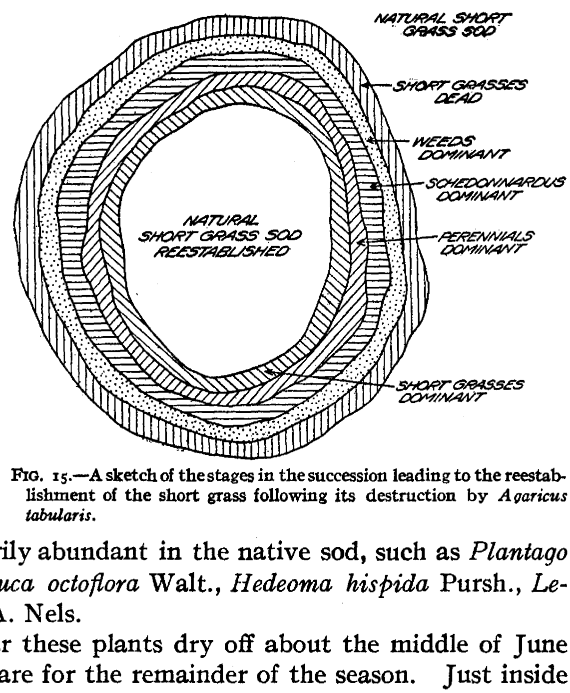

FIG. 15.—A sketch of the stages in the succession leading to the reestablishment of the short grass following its destruction by *Agaricus tabularis*.

During a normal year these plants dry off about the middle of June and the area remains bare for the remainder of the season. Just inside this zone and not sharply separated from it is the inner stimulated zone. This zone is in the second or late weed stage and is dominated by a luxuriant growth of the plants listed in the first stage and the following more characteristic ruderals: *Chenopodium incanum* (S. Wats.) Heller, *Lappula occidentale* (S. Wats.) Greene, *Cryptanthe crassisepala* (T. and G.) Greene, *Amaranthus blitoides* (Wats.).

Following the late-weed stage several of the stages clearly recognized on abandoned roads or cultivated fields can be distinguished.

The third, or short-lived grass, stage is marked by *Schedonnardus panniculatus* (Nutt.) Trel., alone or with *Malvastrum coccineum* (Pursh.) Gray, and *Sitanion hystrix* (Nutt.) Smith.

[1] If deep-rooted perennials such as *Artemisia frigida*, *Gutierrezia sarothrae*, etc., occur in this zone, they occasionally continue to grow, due to a supply of available soil moisture in the deeper layers of the soil.

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The fourth or perennial stage is shown by the entrance of *Gutierrezia sarothrae* (Pursh.) B. and R. and *Artemisia frigida* Willd.

The fifth, or short-grass, stage is established gradually and *Bulbilis dactyloides*, which in this case must depend largely on reseeding, does not predominate over *Bouteloua gracilis*. As a result the two short grasses are established and the final stage reached without the development of the characteristic Bulbilis stage.

In figure 13 a bisect and transect of a ring of *Agaricus tabularis* is shown. The zones here are unusually wide, and the mapping made in 1916 is characteristic of a dry year. Very few annuals appear. During 1915 the early weed stage to some extent, but especially the late weed stages, were marked by a very luxuriant growth and a dense stand. Such annuals as *Festuca octoflora*, and *Plantago purshii* occurred abundantly in every zone and stage of revegetation. This ring is shown because it illustrates the succession stages somewhat better than the narrower rings in which the short-lived grass stage usually occupies a much narrower zone.

The zone of disturbed vegetation is usually about 3 meters broad in these rings of *Agaricus tabularis*. Estimates of the rate of advance of this fungus given earlier in the paper were 12 cm. per year. At this rate the time required for the vegetation to become reestablished would be 300÷12 or 25 years. This estimate is in accord with previous studies in succession on abandoned plowed fields (Shantz, 1911) and on abandoned roadways (Shantz, 1917).

GENERAL DISCUSSION

Under normal conditions in eastern Colorado *Agaricus tabularis* produces an enormous superabundance of spores. From the number and age of the fairy rings which are shown in figure 2, new rings are only rarely formed. Most of the rings are fragments of old rings which have long since ceased to be true or complete circles. The conditions necessary for the germination of spores of *Agaricus* spp. have been the subject of many investigations. More recent summaries and studies (Ferguson, 1902; and Duggar, 1905) show clearly that the conditions most favorable to germination would be seldom realized on the Great Plains. Nor would there be chances of reproduction by fragments of tissue. The effects of the presence of old fruits and mycelium on germination of spores would only tend to cause germination where the mycelium already existed. Only rarely do spores germinate and produce new rings. At first these would not present the appearance of older fairy rings, but would merely represent small more or less circular areas in which sporophores are produced and the native grasses are stimulated (Pl. 30, C.). The mycelium would spread out in all directions as practically all fungi do in culture media. During the first year or two there would be no differentiation into zones, but subsequent gradual outward growth would result in the separation of the zones shown in figure 3 (at A). Outward growth would be slow, approximately 12 cm. a year on an average. This progress would not be regular, but would be wavelike, being comparatively rapid, 30 to 60 cm. during favorable years and very slow or none at all during unfavorable years. The sod would first be stimulated by the increase of available nitrogen, owing to the reduction of the organic matter of the soil, then killed by insufficient soil moisture in the area of dense mycelium. As this mycelium began to decay, the native ruderals would again invade and develop luxuriantly, owing to the abundant supply of readily available nitrogenous material. These ruderals would give way to short-lived grasses, and these in turn to the short grasses of the natural sod. To use a figure already employed by Ritzema Bos (1901), the spread of the mycelium would resemble the spread of a flame started by dropping a match into dry grass. Even if the grass were reestablished at a distance of a meter or so behind the flame, the chances of the flame's striking back would be very remote. We may think of the flame as representing the active mycelium and the grass as representing the organic matter of the soil on which the mycelium feeds.

The fairy ring starts from the point of germination of the fungus spore and spreads outward at approximately an equal rate in all directions. In case of an obstacle, such as an ant hill, or another fairy ring, growth stops at this point. In the case of an ant hill the ring will close in around it as soon as it is passed and tend to regain its original complete form. In case two rings meet they do not continue, but are exterminated at the line of contact. As the fungus filaments spread outward they consume a portion of the organic matter of the soil. Carbohydrates are consumed, and the proteid portion is consumed or changed into amino acids and then to ammonia. The fungus advances and never recedes, since the young growing filaments are always advancing into new soil and since only the old filaments lie on the inside of the ring where the available portion of the organic matter of the soil has already been consumed by the fungus.

The effect of the fungus filaments on the soil is to reduce a part of the organic matter to ammonia, which is combined to form ammoniacal salts or is converted by bacteria into nitrites and later into nitrates. When the mycelium dies, it is reduced by bacterial action to ammonia, which may later be built up into nitrates. The increase in available nitrogenous material in the soil occupied by the young mycelium stimulates the growth of the grasses or other plants, which consequently make greater demands on the soil moisture. When this is once exhausted (in *Agaricus tabularis*), the mass of fungus filaments prevents the penetration of rain water. The intense drouth to which plants are thus subjected kills off the buffalo and grama grasses and the other plants which may be associated with them. The area is thus left bare for the invasion of other plants. The mycelium after a few years dies, leaving the soil still more enriched and no longer impervious to water.

The first stage in the succession on this bare area is (1) an early-weed stage, followed by (2) a late-weed stage. This is followed by a (3) short-lived grass stage, and this by a (4) perennial stage, which gives way to the (5) original short-grass cover.

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PLATE 10

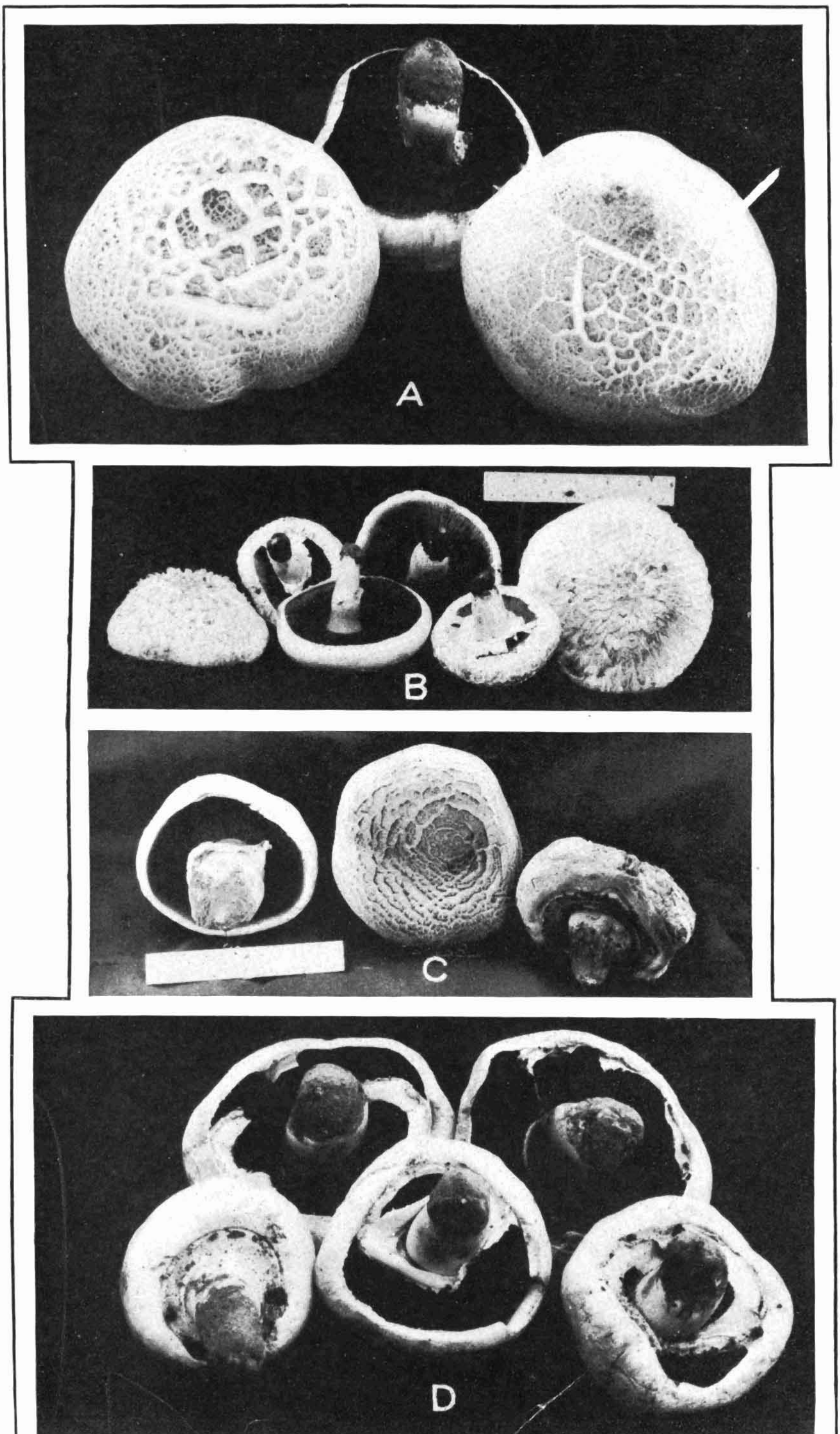
Agaricus tabularis:

A.—Three fruiting bodies about 10 to 15 cm. in diameter showing variation in the pileus. Akron, Colo., June 14, 1915.

B.—Large, firm, fleshy fruiting bodies 10 to 15 cm. in diameter. Akron, Colo., July 7, 1909.

C.—Three typical fruiting bodies. From left to right these weighed respectively 207, 298, and 163 gms. each. The largest was about 17 cm. in diameter. Akron, Colo., July 12, 1909.

D.—Bottom view of fruits 7 to 15 cm. in diameter. Akron, Colo., June 14, 1915.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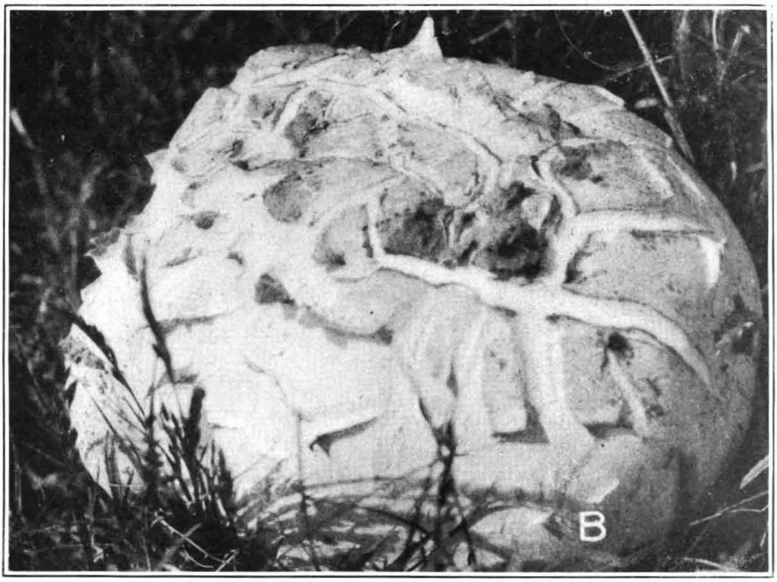
A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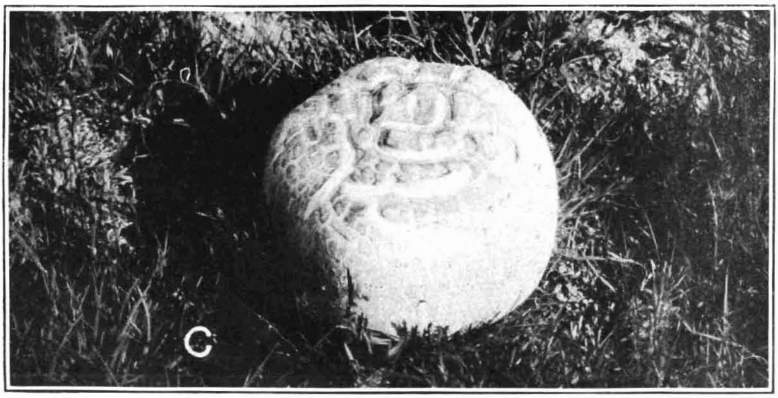
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PLATE 11

Agaricus tabularis:

A.—Sporophores developed in a dense stand of *Agropyron smithii*, which protected them from rapid drying. In this location the tops were smooth. The fruiting body was 12 cm. in diameter.

B.—Sporophore from the same ring as figure A, but freely exposed and showing the rough scaly top. The fruiting body was about 12 cm. in diameter.

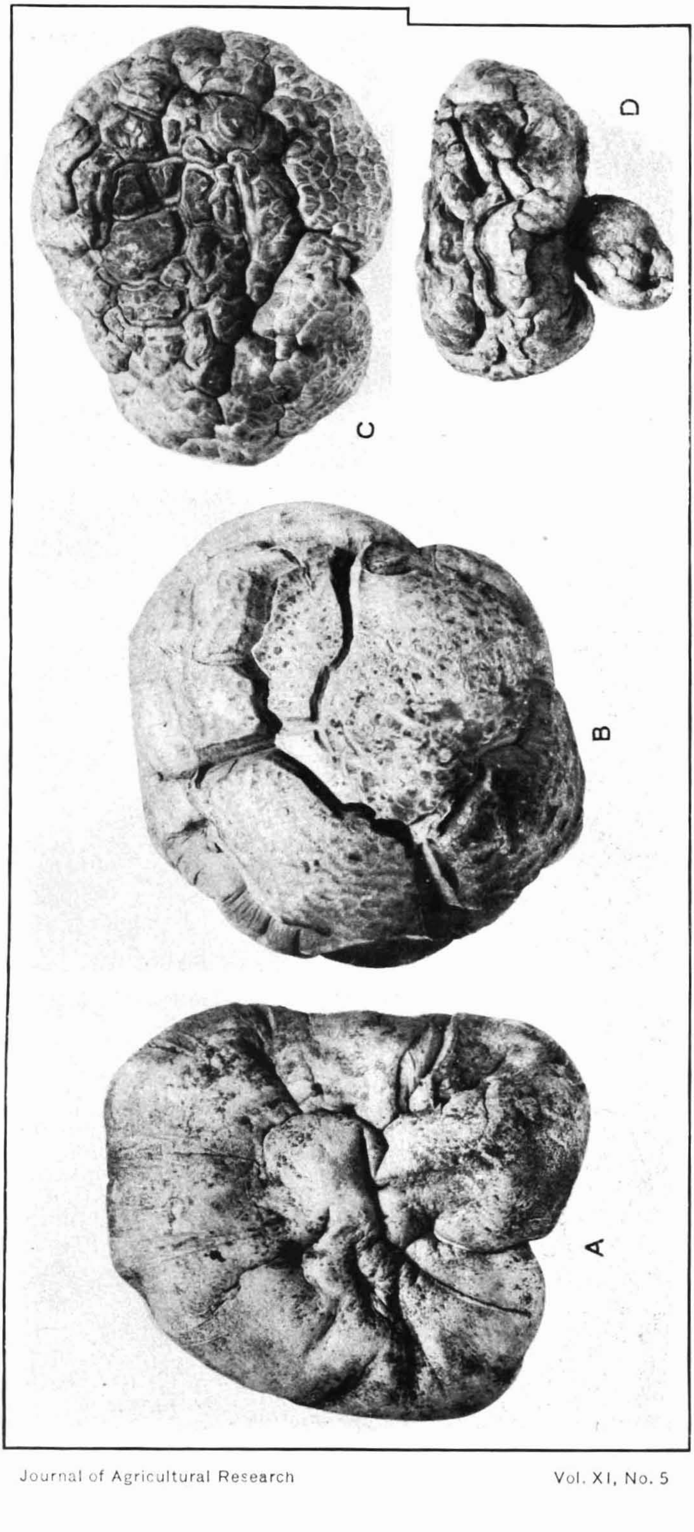
C.—Typical of fruiting bodies exposed on dry hot days. Fruiting bodies 10 cm. in diameter. The figures of Plate 11 show variation in pileus. Akron, Colo., June 15, 1916.

PLATE 12

Agaricus tabularis:

A, B.—Two fruiting bodies showing smooth and nearly smooth pileus. Greatest diameter, 11 cm. Akron, Colo., 1915.

C, D.—Two fruiting bodies showing the rough or tabular structure of the pileus. Greatest diameter, 9.5 cm. Akron, Colo., 1915.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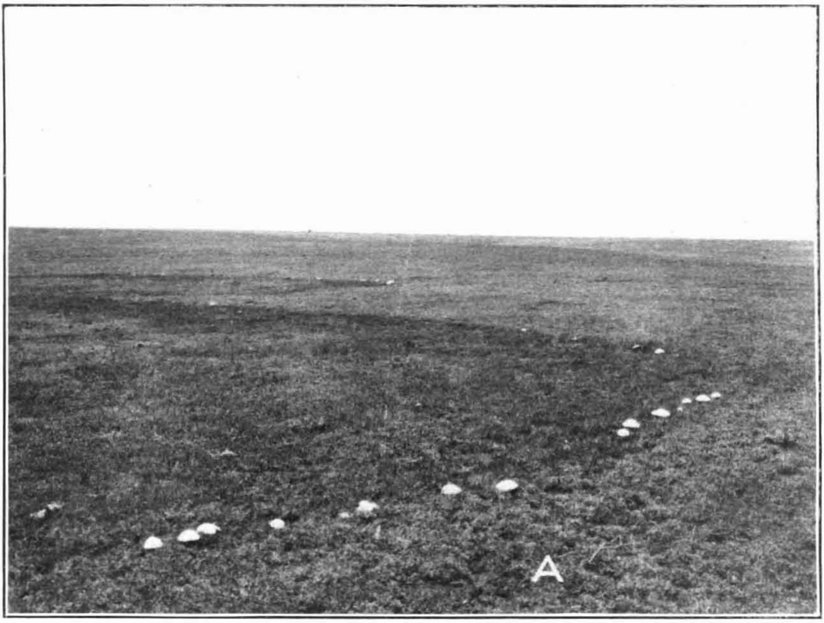


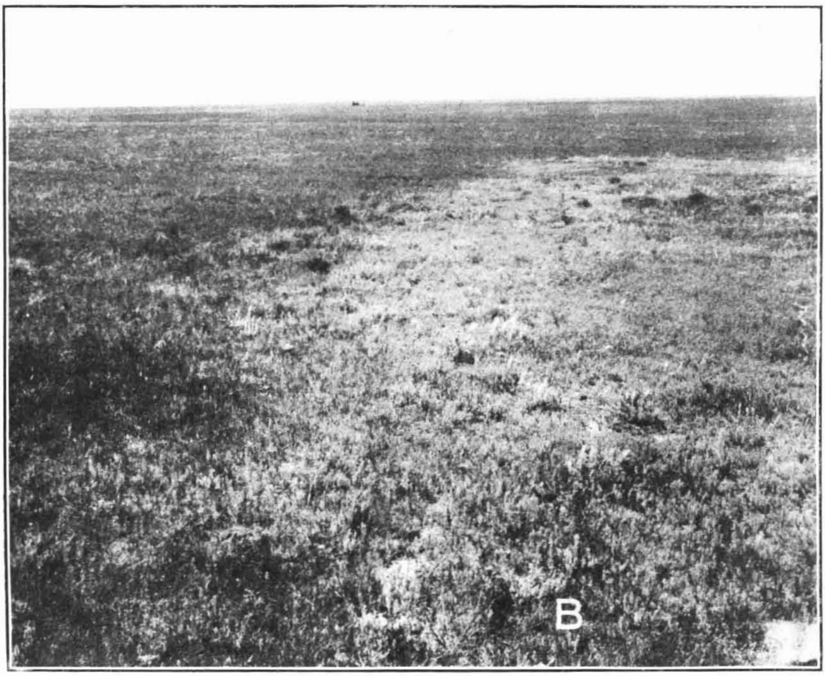


PLATE 13

Agaricus tabularis:

A.—Two fruiting rings showing large fruiting bodies about 15 cm. in diameter and of relatively uniform size. Akron, Colo., June 7, 1909.

B.—A ring just after the fruiting period. The area in the ring is distinguished by dead short grass with small plants of *Plantago purshii* and *Festuca octoflora* and unusually luxuriant plants of *Artemisia frigida*, the roots of which penetrate below the dry soil layer of the ring. The inside of the ring is marked by the abundance of annuals, of which *P. purshii* is the most prominent and abundant. Akron, Colo., June 25, 1915.

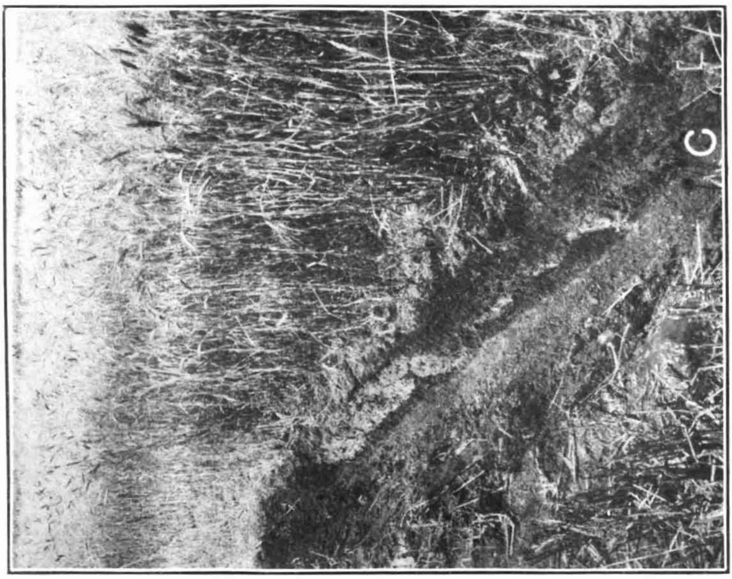
PLATE 14

Agaricus tabularis:

A.—A fruiting ring. The vegetation outside of the ring is pure short grass with *Festuca octiflora* and *Plantago purshii*. At the outer edge of the ring 18 mushrooms occur in the portion shown in the photograph. Just back of the fruiting area the short grass is dead or dying. In this area there are a few very small plants of *P. purshii*, *Lepidium ramossissimum*, and *Chenopodium incanum*. The inside shows a rank growth of *L. ramossissimum*, *Lappula occidentale*, *P. purshii*, and *Festuca octoflora*. Akron, Colo., June 14, 1915.

B.—The mycelium as it appears on the soil mass. So dense is this fungus growth that all crevices in the soil are filled with white hyphæ. Water penetrates very slowly into a dry soil in this condition. Akron, Colo., August 14, 1915.

C.—A trench across a ring of *A. tabularis* in a Kubanka wheat plot, showing the mycelium in the soil. A sketch of this trench is shown in figure 14. The mycelium in the ring fills the soil lying from 10 to 30 cm. in depth. The ring is about 4 meters wide, and on the inside of this area the mycelium occurs sparingly at a depth exceeding 30 cm. The mycelium may have grown down as it died above. The soil is very dry in the mycelium area, but moist where no mycelium occurs. The available water was 0.6 per cent in the mycelium and 11.6 per cent in the soil outside the mycelium area. After a rain the soil above the mycelium remained very wet, owing to the failure of moisture to penetrate the dry mycelium layer. Only that portion of the soil above the mycelium (3 or 4 inches) was moistened by the rain on August 6 and 7 of 1.89 inches, while the soil in the adjacent areas was wet to a depth of over 1 foot. Akron, Colo., August 10, 1915.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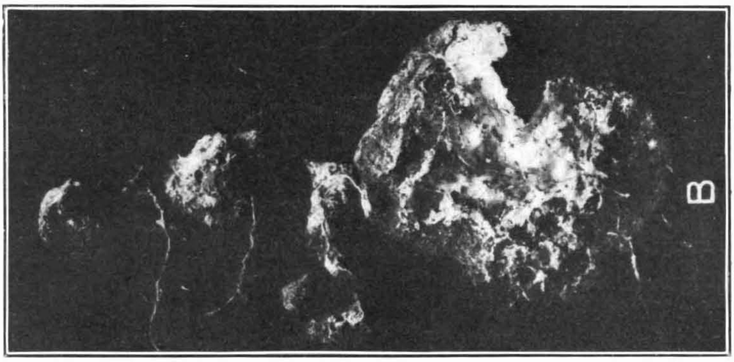
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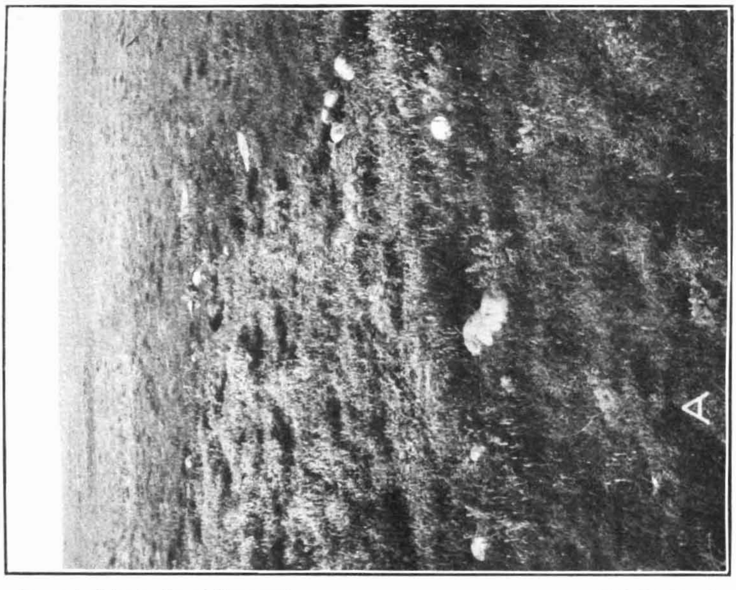
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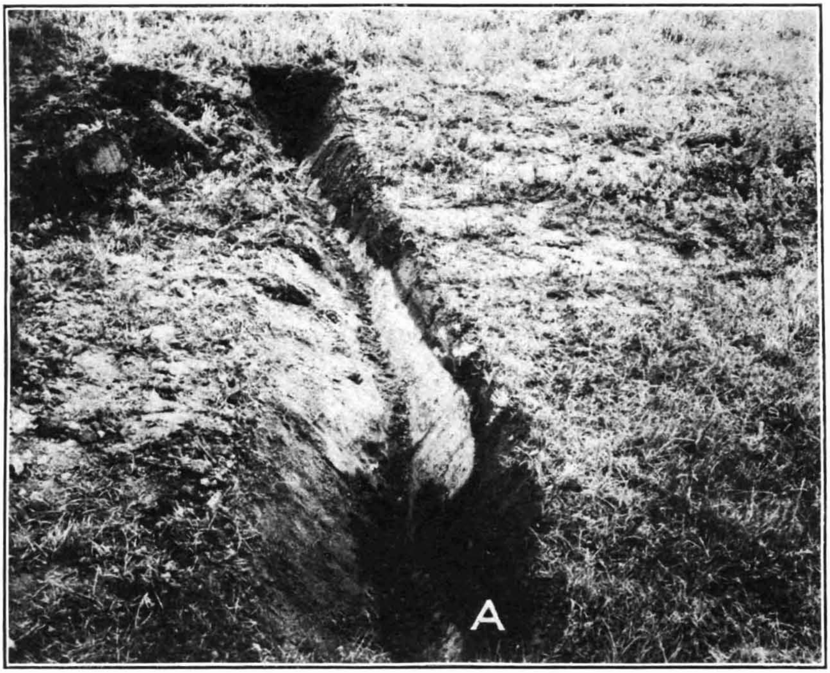
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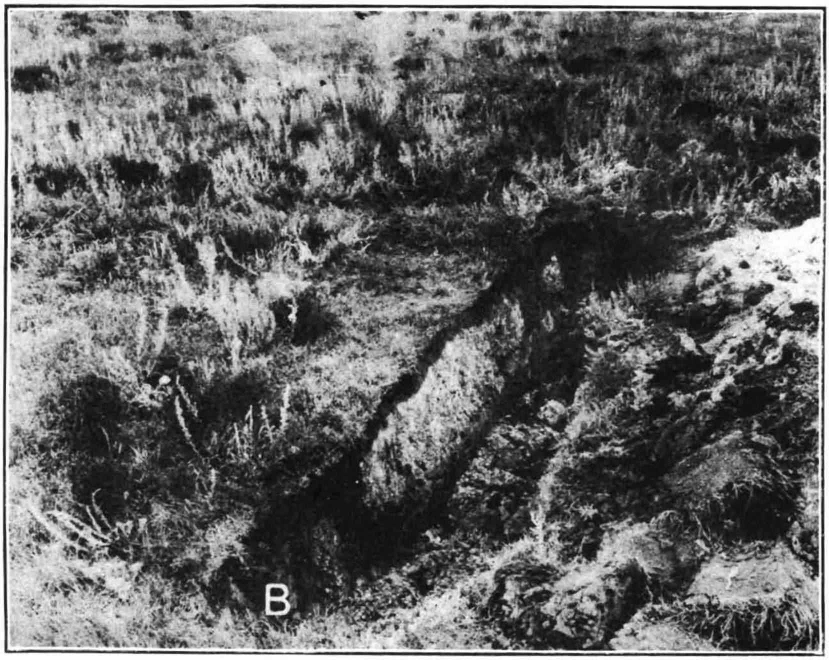

B

PLATE 15

Agaricus tabularis:

A.—A trench across a fairy ring. This reproduction of a photograph which was taken after a rather heavy rain shows the dry soil area (light-colored) in the ring and extending back inside the ring. The darker soil above is freer from mycelium, while the light soil is filled with a dense growth of mycelium. In the foreground the moisture has penetrated around the end of the mycelium and back underneath, showing distinctly the difficulty with which the dry soil filled with mycelium is wetted. The mycelium comes to within 2 or 3 inches of the surface of the soil, and is usually about 1 foot in advance of the fruiting bodies. Akron, Colo., August 2, 1915.

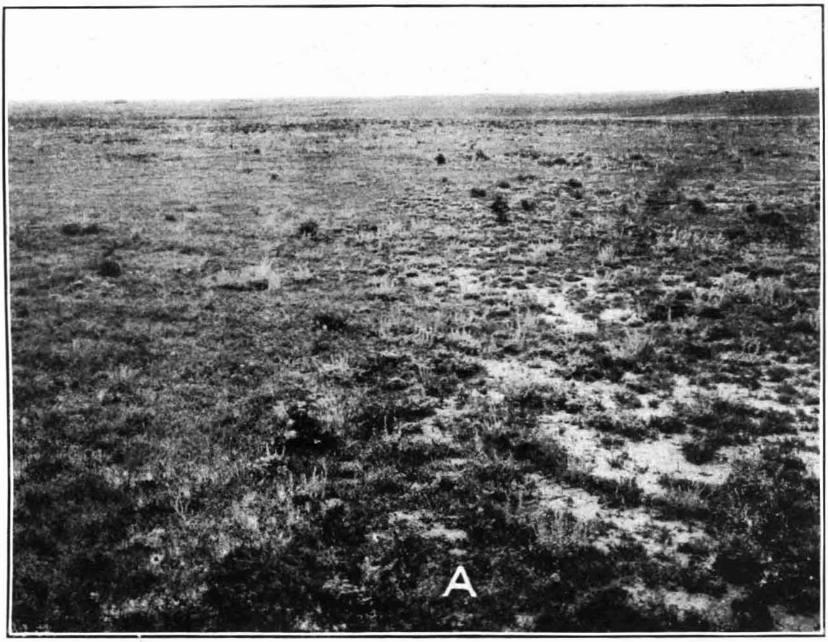
B.—Another trench showing a different distribution of the mycelium in the soil. Akron, Colo., August 2, 1915.

PLATE 16

Agaricus tabularis:

A.—General appearance of a fairy ring formed by *A. tabularis* during a dry year. The bare zone shows clearly at the right. Scattered through this are a few remnants of the short grass and also a few plants of *Artemisia frigida.* The roots of the latter are partly below the soil occupied by the mycelium. Just at the left of this bare area the grass is closely cropped and withered. This is the outer stimulated zone of wet periods. The illustration does not show the difference between this zone and the normal vegetation at the left. Akron, Colo., August 7, 1916.

B.—General view of a ring formed by *A. tabularis;* photographed during a dry year. The vegetation at the left is normal. Just at the right the withered zone extends to the lower right corner of the figure. The vegetation is dry and a little lighter colored in this zone. Several old sporophores produced in 1915 are still found in this zone. The darker area at the right is the bare zone and within this the inner stimulated zone, which, because of the dry period, is not luxuriant. A detailed transect and bisect of this ring are shown in figure 13. Akron, Colo., June 11, 1916.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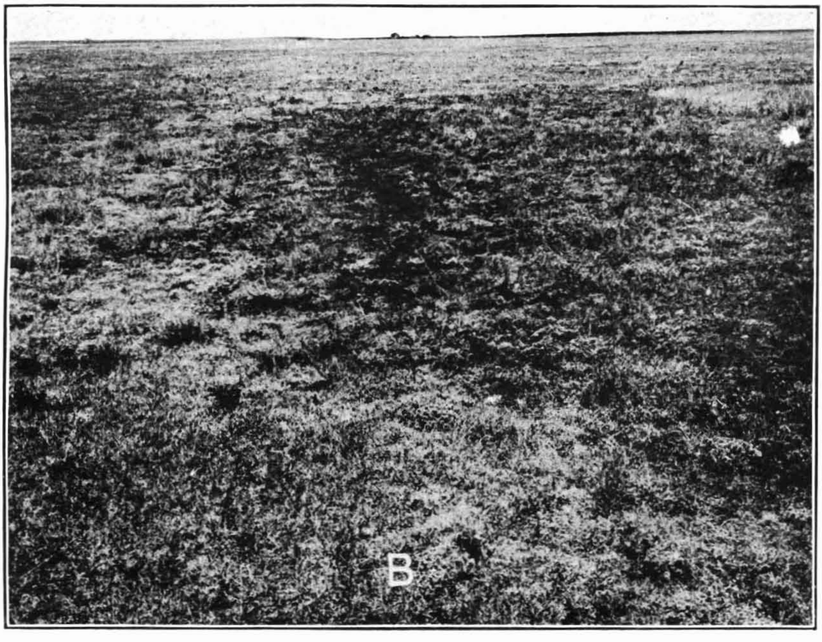
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B

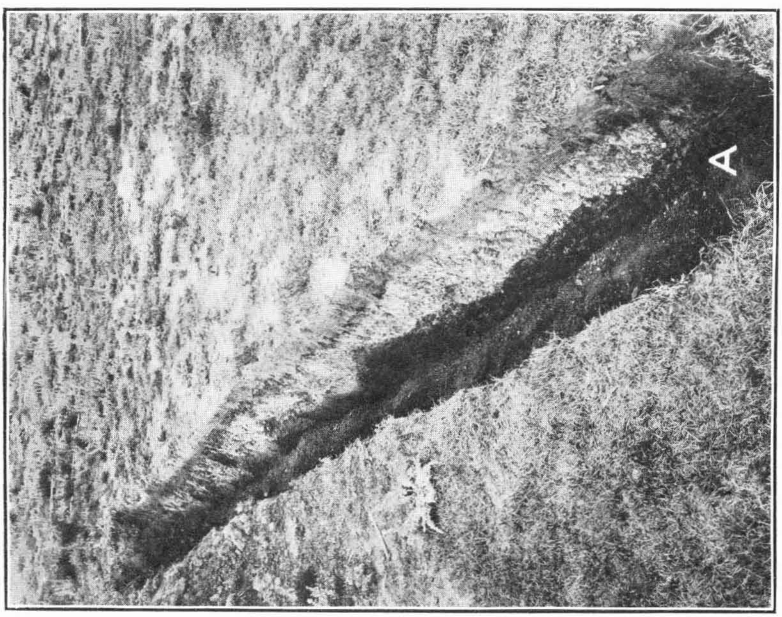
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PLATE 17

Agaricus tabularis:

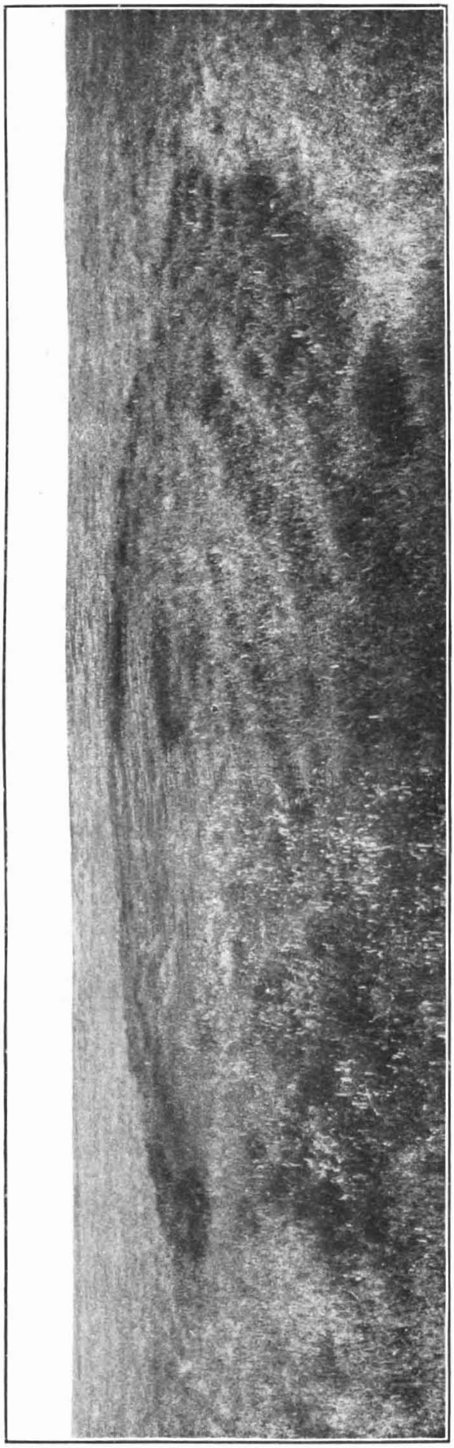
A.—A trench through the ring shown in Plate 16, A. The lower end of the trench is the outside and the upper end the inside of the ring. The outer withered zone lies above the mass of mycelium shown at the right of the picture. The mycelium extends back under the bare zone and becomes more or less interrupted just inside this zone. Akron, Colo., August 7, 1916.

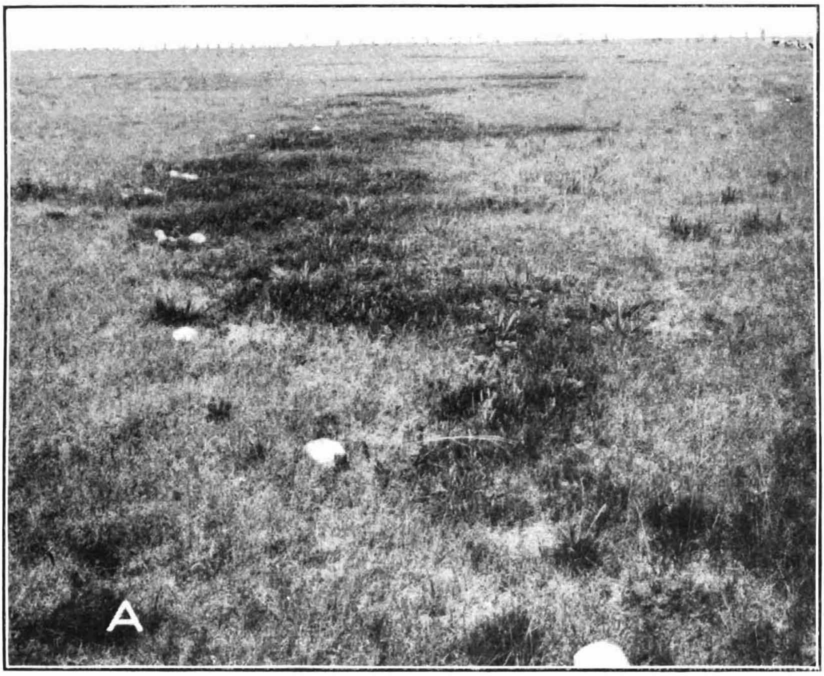
B.—A trench through the ring shown in Plate 16, B. The lower end of the trench is the outside, the upper the inside of the ring. The mycelium is shown extending nearly to the right end of the trench. The dense mycelium in the center of the illustration lies under the bare area. A sketch of this trench is shown in figure 13.

PLATE 18

Agaricus tabularis:

A ring which produced only a few mushrooms in 1915. It is marked by the stimulated growth of *Festuca octoflora*. In this stimulated area three distinct maxima can be distinguished which form concentric rings. The first maximum occurs just inside the fruiting zone, the second about 2 feet inside, and the third about 4 feet inside the fruiting zone.





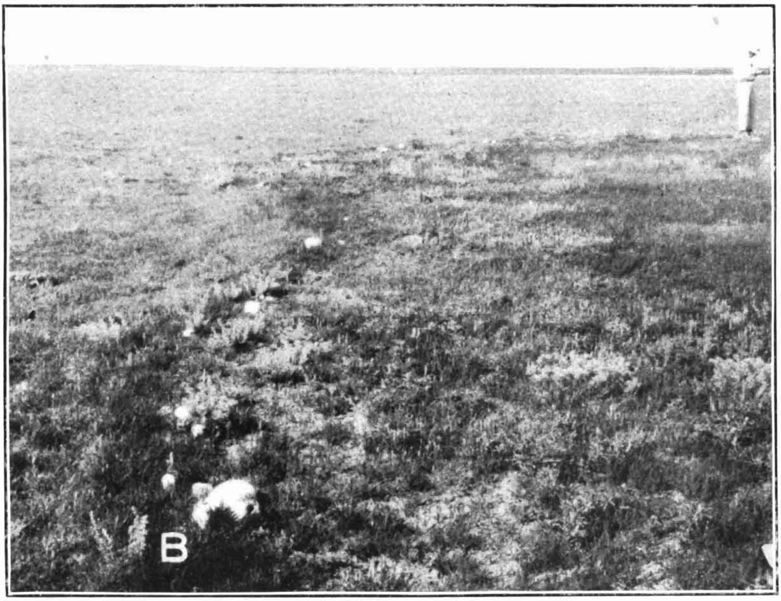


PLATE 19

Agaricus tabularis:

A.—Part of a large ring, showing 42 mushrooms. The area just inside the fruiting zone is marked by dead or dying short grass. Inside this dead zone is a stimulated area chiefly characterized by *Festuca octoflora.* Akron, Colo., June 15, 1915.

B.—A large ring, showing 75 fresh mushrooms. There are also 47 dry mushrooms. Outside the ring the vegetation is typical short grass. A narrow stimulated area, marked largely by *Festuca octoflora* extends several inches in advance of the fruiting zone. Just inside the fruiting zone the short grass is dead. Inside this dead zone the vegetation consists largely of annuals and *Malvastrum coccineum,* with short grass slowly becoming reestablished at a distance of about 4 meters inside the fruiting zone. Akron, Colo., June 14, 1915.

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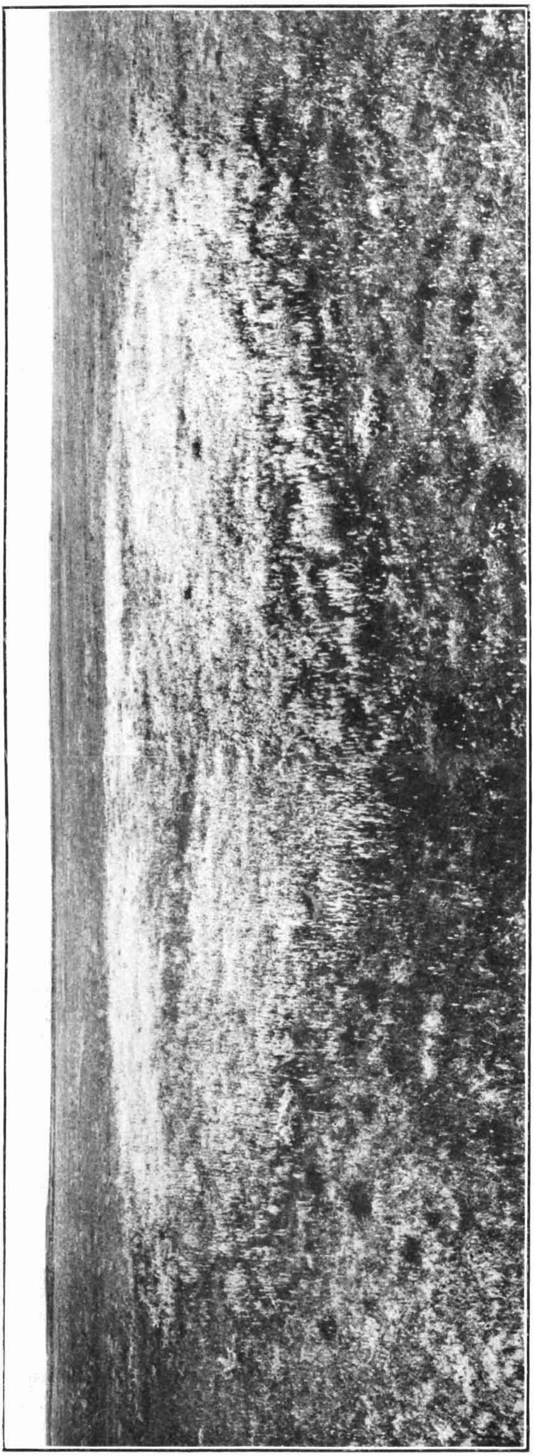
PLATE 20

Agaricus tabularis:

A ring caused by *A. tabularis* and distinguished by a uniform growth of *Plantago purshii.* This plant is almost as abundant outside of the ring as inside, but outside it is very small and therefore not as noticeable. This is a relatively small ring, and the stimulation extends to the center. Akron, Colo., June 14, 1915.

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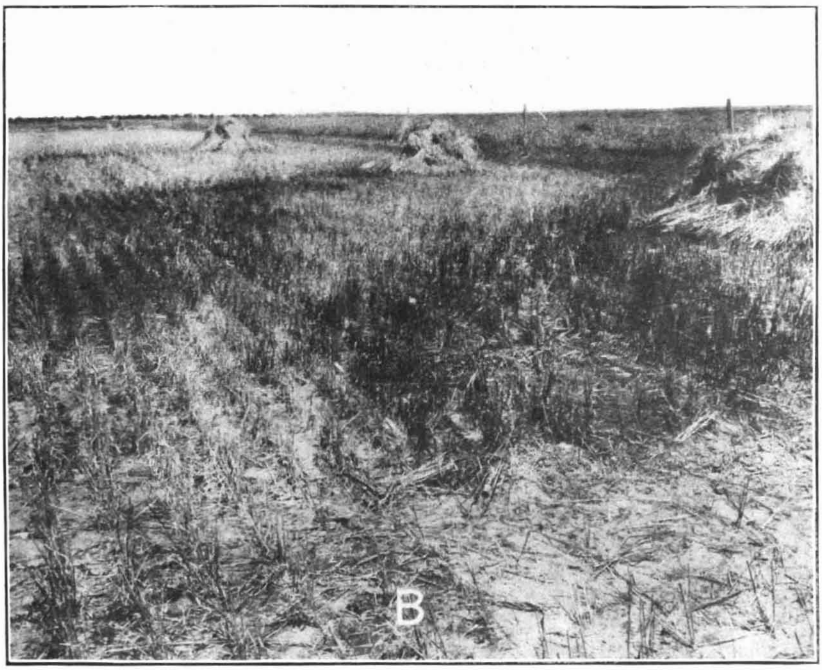

B

PLATE 21

Agaricus tabularis:

A.—Effect of a ring on Kubanka wheat. The wheat at the left shows normal production on the plot; at right, the straw is weak, the heads are poorly filled and prematurely ripened. The yield of dry matter at the left was 500 gm. per square meter; at the right, 400 gm. Even a greater difference was shown in the yield of grain, that in the ring being 63 gm. and that outside being 137 gm. per square meter. In this case the yield in dry matter inside was only 80 per cent of that outside and the yield of grain only 46 per cent. Akron, Colo., August 10, 1915.

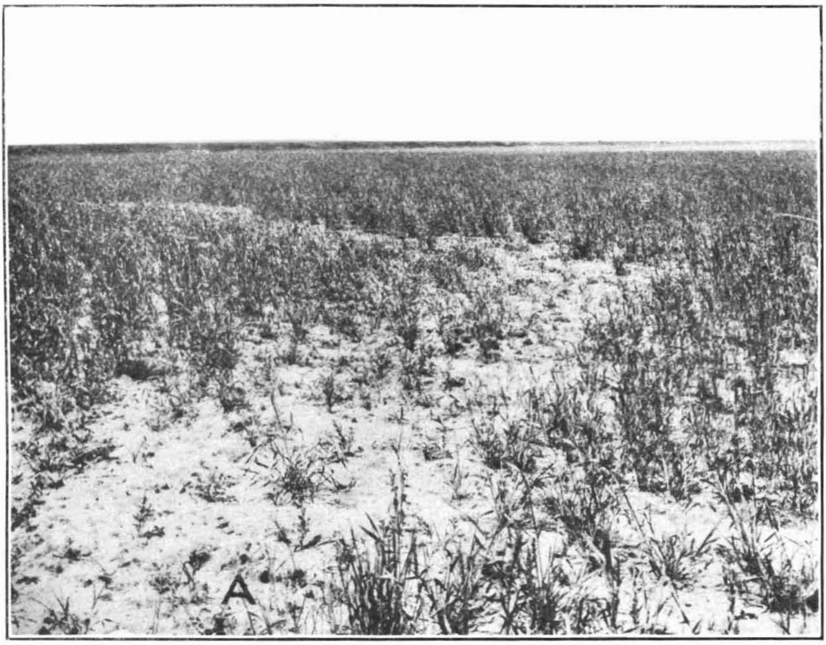
B.—The stubble showing the distribution of the ring of *A. tabularis*. The wheat ripened off early in the ring, and the straw turned dark. The farther end of the trench shown in figure 2 ended at about the middle of the foreground of this picture. Akron, Colo., August 16, 1915.

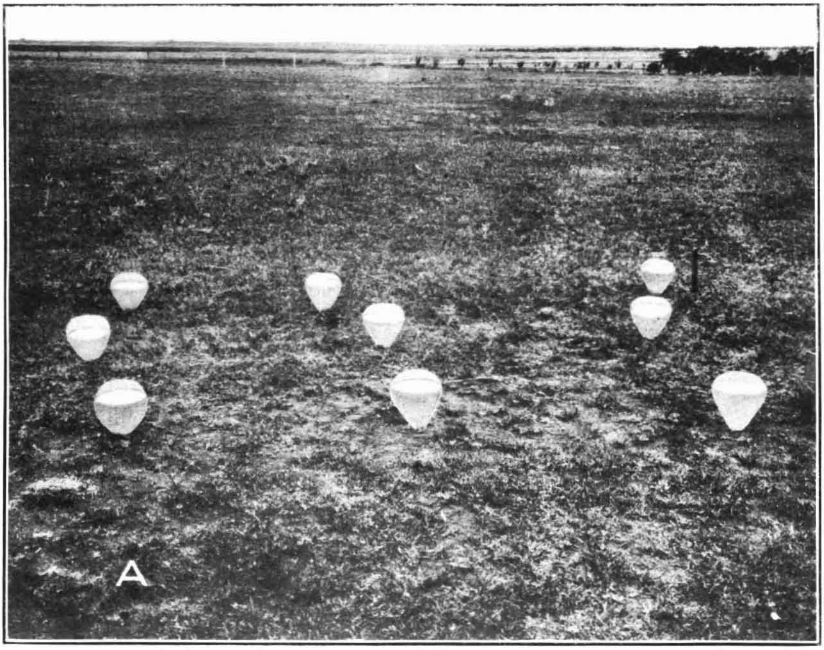
PLATE 22

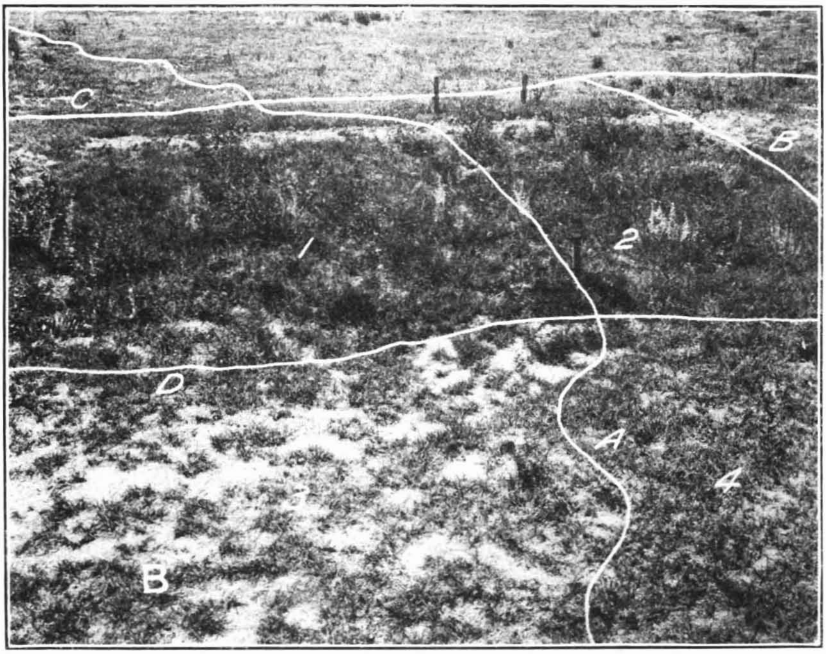
Agaricus tabularis:

A.—A ring formed by *A. tabularis* in a field of Turkey wheat. The bare zone is the only prominent zone in this ring. The dry season prevented the development of luxuriant growth on the stimulated zones. Akron, Colo., June 10, 1916.

B.—A trench across the ring shown in the figure above. The soil under the bare zone was permeated with the mycelium and was very dry. Akron, Colo., July 18, 1916.



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B
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2
D
A
4
B

PLATE 23

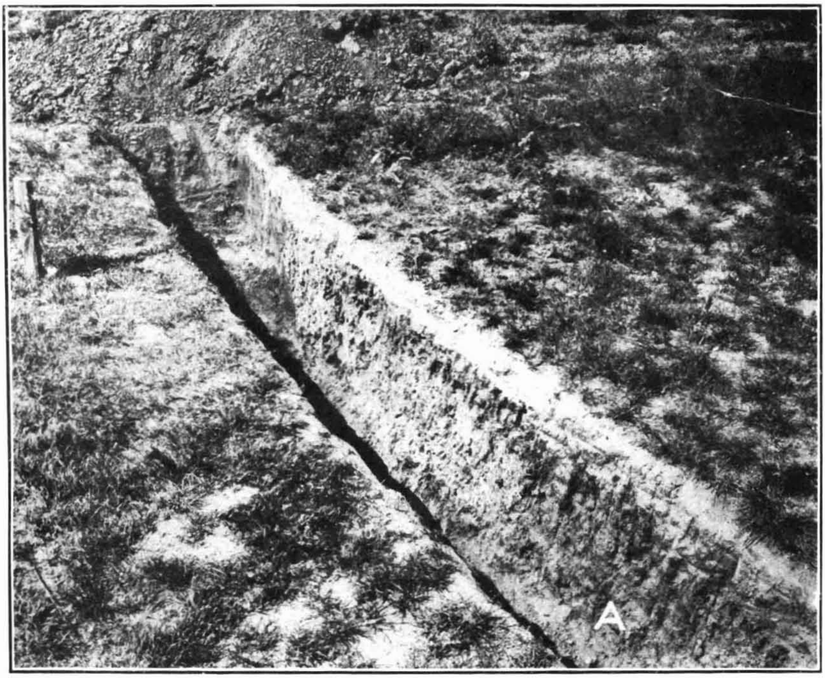
A.—Method of measuring the penetration of water in three zones of a ring of *Agaricus tabularis*. The first three 2-liter flasks in the foreground are in the bare zone, the second three are in the withered zone, and the three in the background are outside. Those in the bare and withered zones are still almost full of water while those outside in the natural sod are empty. Akron, Colo., July 13, 1916.

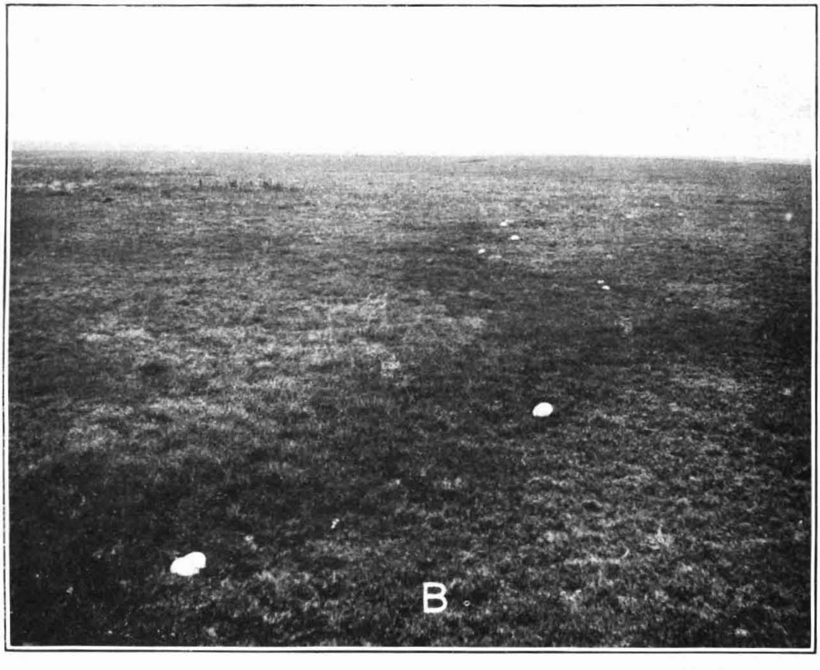
B.—A ring of *Agaricus arvensis* showing the effect of irrigation during a dry year on the different zones. At this period the vegetation both in the zones of the ring and in the native sod was entirely dormant, due to drouth. On this account the withered zone could not be distinguished from the other vegetation. The effect of the surface flooding was marked between the lines C and D. The outer edge of the bare zone is marked by the line A and the outside of the irrigated area by the line B. The area 3 represents the bare zone during a dry year and was in the same condition as that of area 1 at the beginning of the experiment. The effect of irrigation on the natural sod is shown by comparing area 2 with area 4. It is clear that, although the vegetation in area 3 was dying out owing to drouth, if water was continually supplied in quantities sufficient to keep the surface soil continually moist the grasses and other plants grew luxuriantly, indicating that the chief cause of the death of the vegetation was the deficiency in soil moisture. In the background of areas 1 and 2 is shown the trench illustrated in Plate 20, A. Akron, Colo., August 14, 1916.

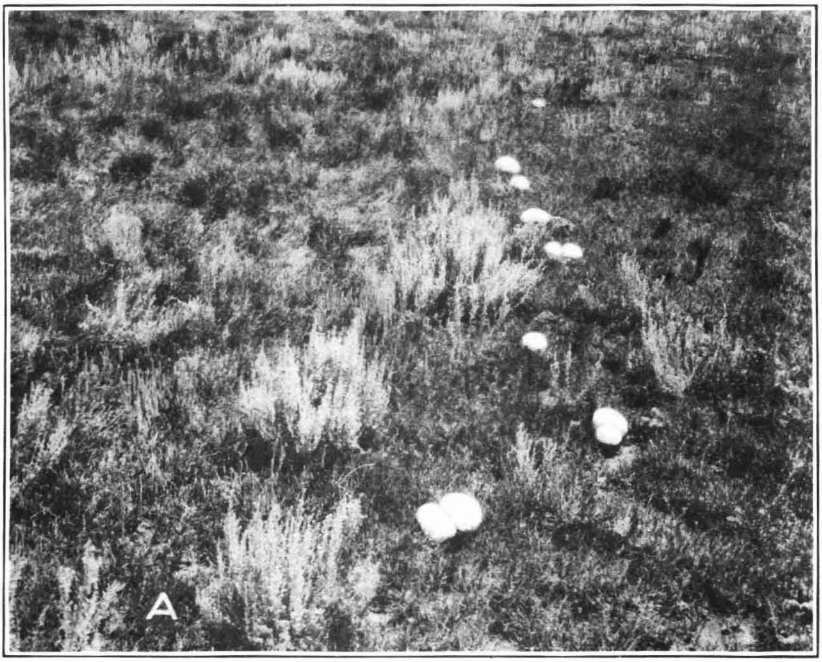
PLATE 24

A.—A trench across the irrigated plot shown in Plate 19, B. Although water had been added continuously as rapidly as it was taken up by the soil, there was no penetration into the mycelium area, which still remained very dry. The growth of the native plants in this area was due entirely to the water available in the upper 3 or 4 inches of soil. Akron, Colo., June 28, 1916.

B.—A ring of *Calvatia cyathiformis* photographed August 21, 1907, 16 miles north of Cheyenne Wells, Colo. The ring is not complete; 16 of the 27 fresh puffballs should show in this illustration. Fifty-six sterile bases, the remnant of an earlier crop, were found in the same zone occupied by the fresh fruiting bodies. Although much of this section of country suffered severe drouth in 1907, recent rains had caused hundreds of these Calvatia rings to fruit. This ring was fully 200 meters across.






A


B

PLATE 25

Calvatia cyathiformis:

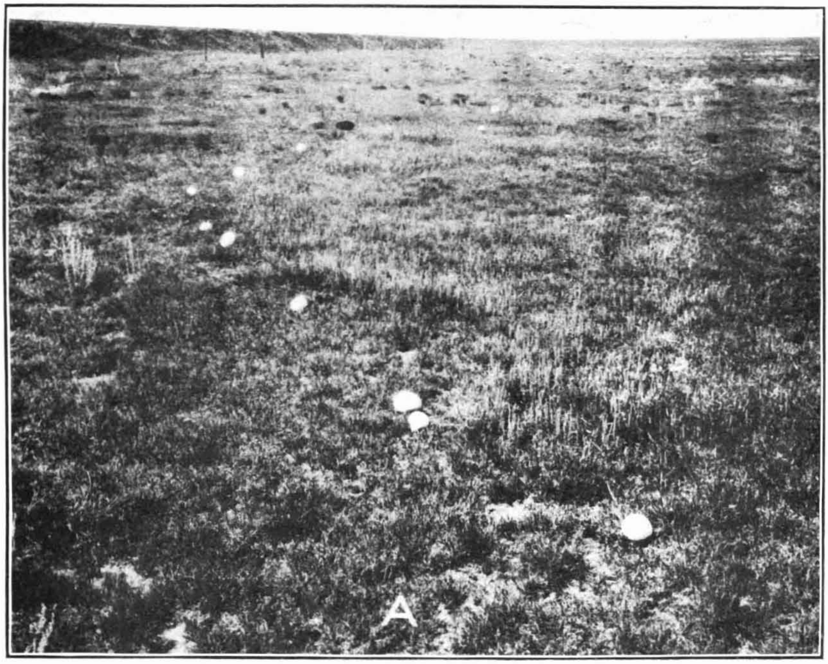
A.—A ring showing stimulation of native plants inside the fruiting zone. The plants showing increased growth are the annuals *Plantago purshii*, *Festuca octoflora*, *Lepidium ramosissimum*, etc., and the perennial short grasses and *Artemisia frigida*. The fruits are well in advance of this stimulated zone. The advance here is from left to right. The second crop of puffballs is seen. Akron, Colo., August 16, 1915.

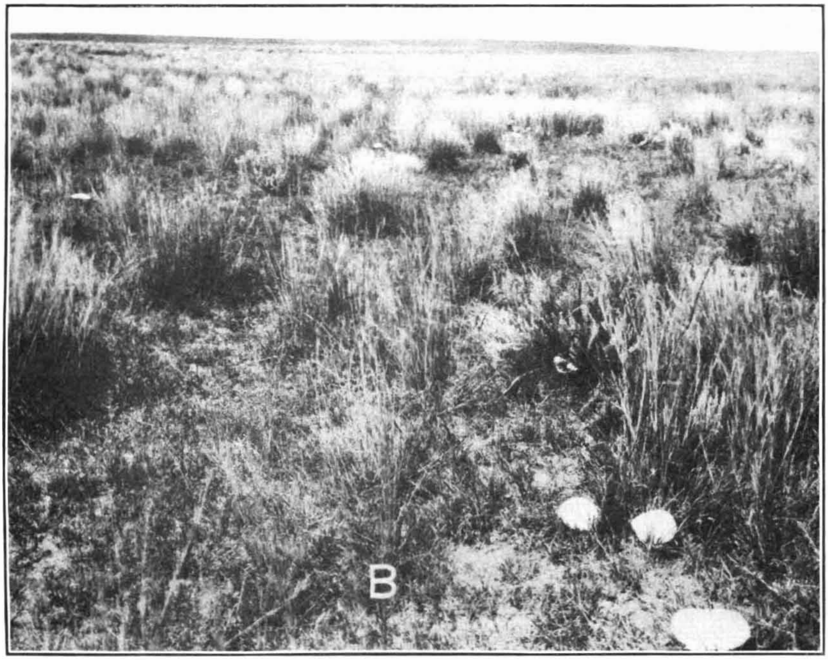
B.—A trench through fruiting zone of *C. cyathiformis*. The soil is moist throughout, owing to recent rains. The mycelium can be distinguished with difficulty and does not render the soil impervious to water as does the mycelium of *Agaricus tabularis*. Fruiting bodies are seen about 30 cm. ahead of the stimulated area in which *Plantago purshii* shows greatest response. Akron, Colo., August 16, 1915.

PLATE 26

A.—A ring of *Calvatia cyathiformis* producing a second crop of puffballs. The sterile bases of the June crop are still present and occur in the outer edge of the stimulated area. Eleven fruits and ten old stumps occur in the same portion of the ring. This ring is shown in figure 2 as ring 5. The stimulated effect is shown chiefly in the *Plantago purshii*, and is evident for a distance of 1.5 meters in the ring. The first crop appeared at the very edge of this area. The second crop shown in this illustration is about 30 cm. in advance of this area. Akron, Colo., August 16, 1915.

B.—A large ring formed by *Lepiota morganii*, showing a second crop of fruiting bodies. The sketch of this ring (fig. 7) shows 10 fresh and about 50 dry fruiting bodies from the earlier crop. The vegetation is largely *Andropogon scoparius* and *Bouteloua hirsuta*, but no effect from the presence of the fungus is noticed on the native growth. The ring is about 24 meters across and forms an almost perfect circle. The soil is sandy. The young fruiting bodies are about 15 cm. in advance of the old. Twelve miles southeast of Yuma, Colo., August 17, 1915.





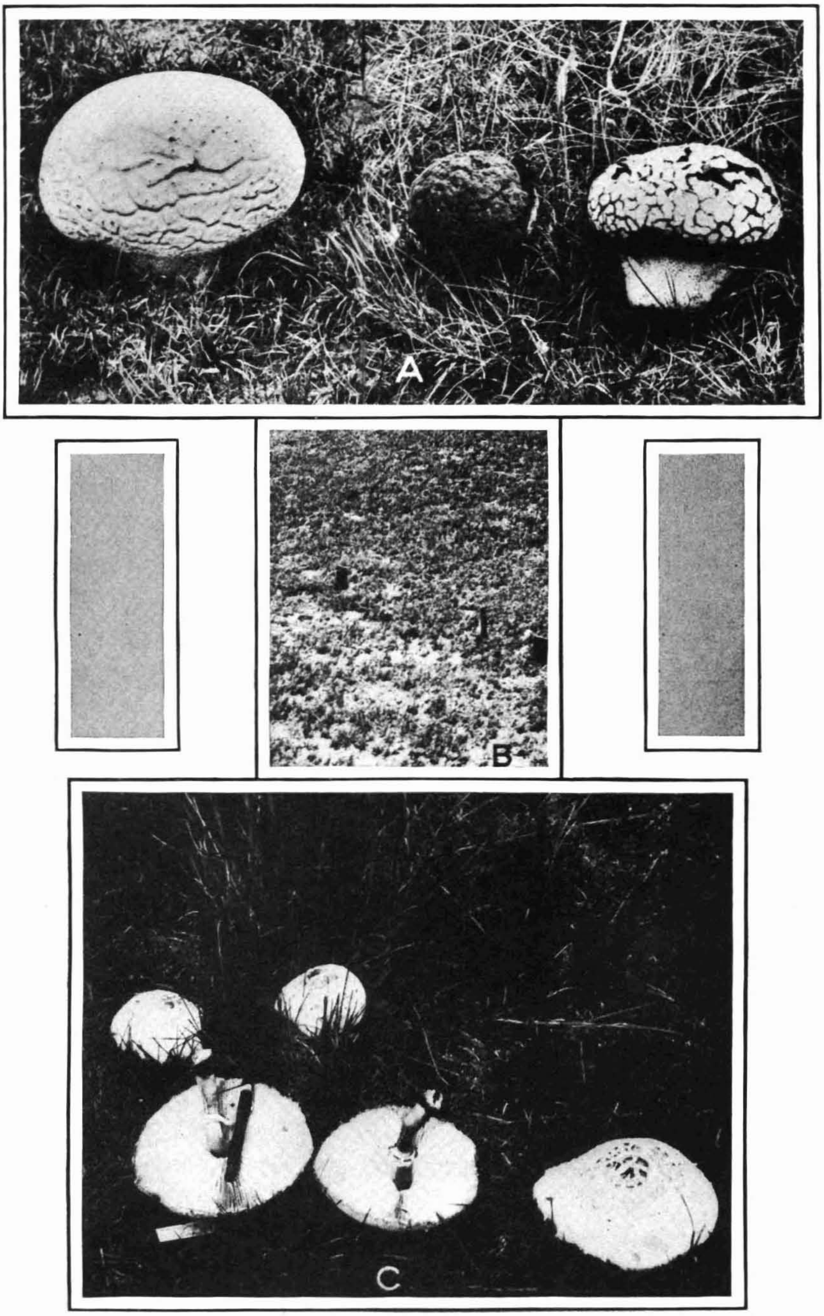

A
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PLATE 27

A.—Three stages in the ripening of sporophores of *Calvatia cyathiformis*. The fruiting body at the left has just formed, and the flesh is still white and in good condition to eat. The peridium is already strongly marked. The fruiting body at the right is at least 2 days older, and the peridium is breaking off in rather thin plates. In the center is a still older fruiting body from the upper part of which the peridium has blown away, exposing the spore mass. The diameter of largest fruiting body is 15 cm.

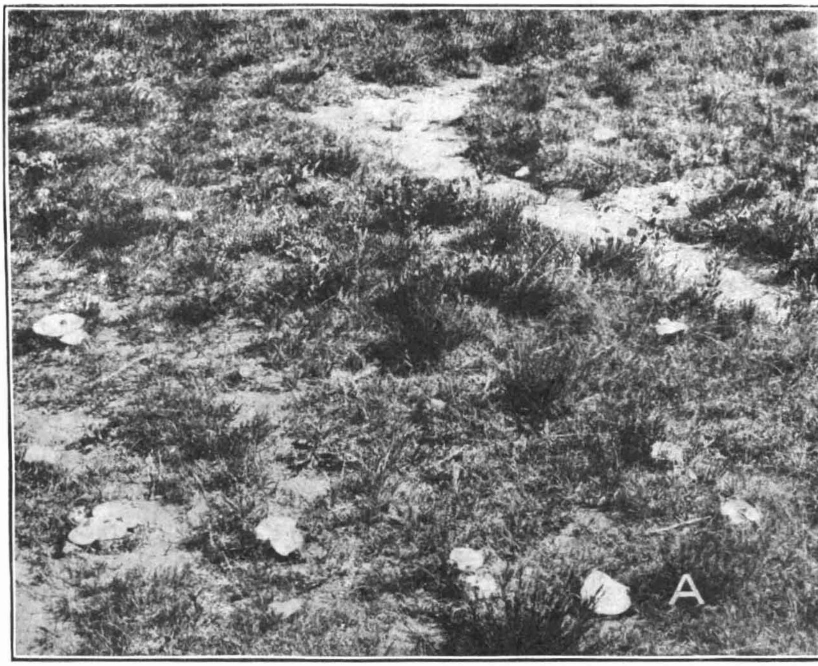
B.—Effect of a ring of *C. cyathiformis* on the density of the short-grass sod. The area behind the short stakes is in the stimulated zone, while that in the foreground is in the natural sod. The effect here has been to thicken the sod cover. Akron, Colo., June 10, 1916.

C.—Three fruiting bodies of *Lepiota morganii* in place in the fairy ring shown in Plate 22B, and sketched in figure 7, and two fruiting bodies inverted. These fruiting bodies are from 12 to 20 cm. in diameter.

PLATE 28

A.—A small ring formed by *Agaricus campestris*, showing a total of 29 mushrooms, the largest being about 10 cm. in diameter. The footpath in the upper right portion of the illustration has no connection with the ring. Akron, Colo., June 17, 1916.

B.—A large ring of *Calvatia polygonia*, showing 14 fruiting bodies, the largest of which are 33 cm. in diameter. The diameter of this incomplete ring was about 100 meters. The puffballs occurred at the edge of a very green area of short grass. No difference in composition of the native was noted, but the deep-green color and the somewhat more luxuriant growth of the short grasses just inside the fruiting zone was especially noticeable. Six miles southwest of Yuma, Colo., July 26, 1907.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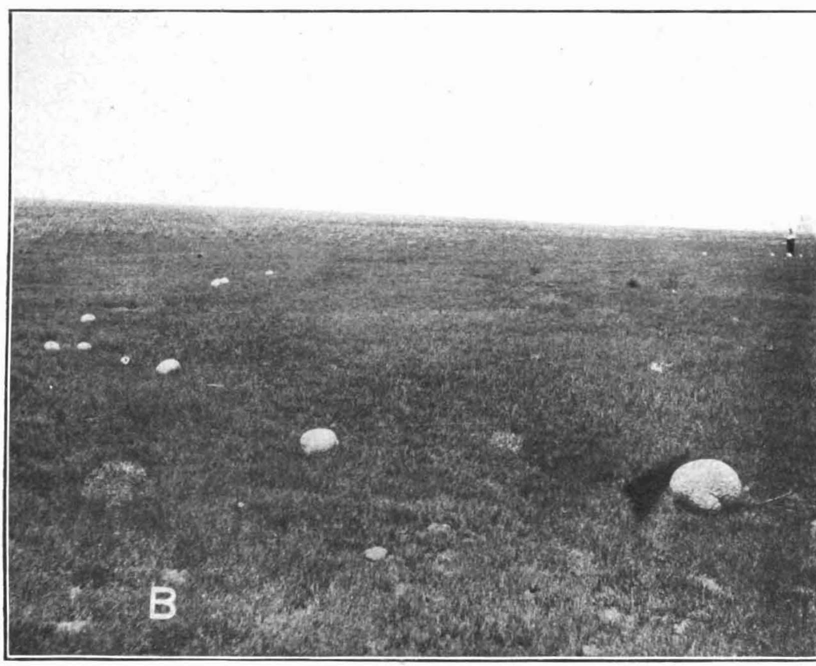
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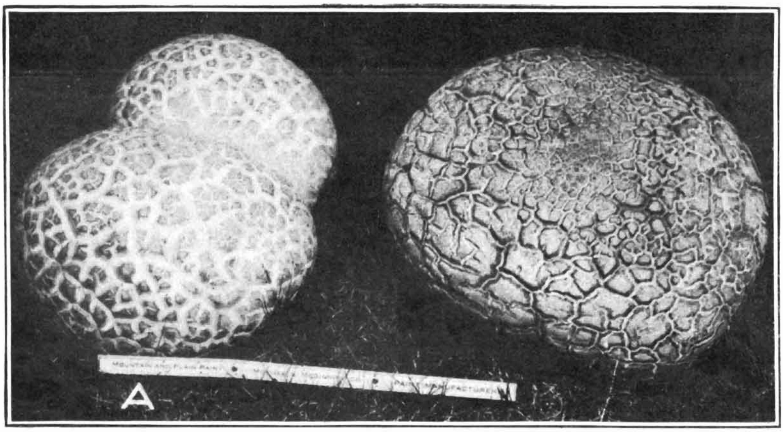
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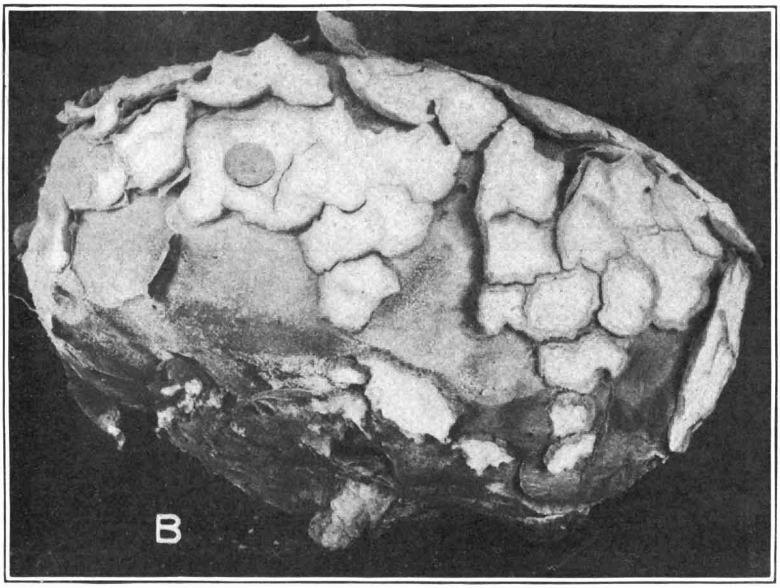
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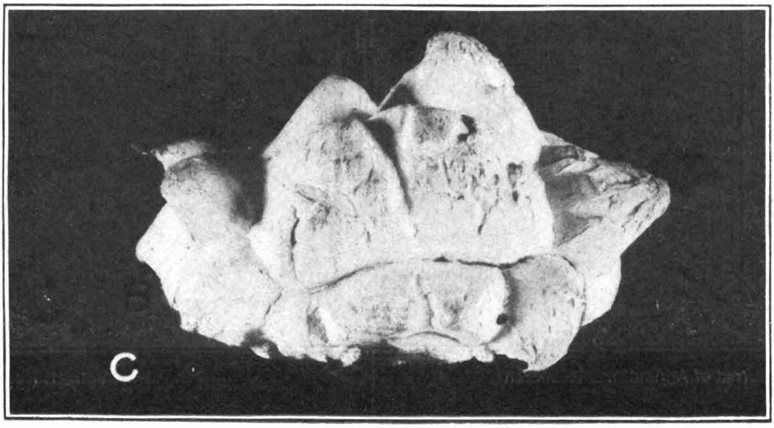

C

PLATE 29

Calvatia polygonia:

A.—Two fresh fruiting bodies showing the character of the peridium at different stages. The fruiting body at the right is 30 cm. in diameter and is a little older than that at the left. Yuma, Colo., July 20, 1907.

B.—An old fruiting body dried in place, showing the thick peridium scales. Diameter 28 cm.

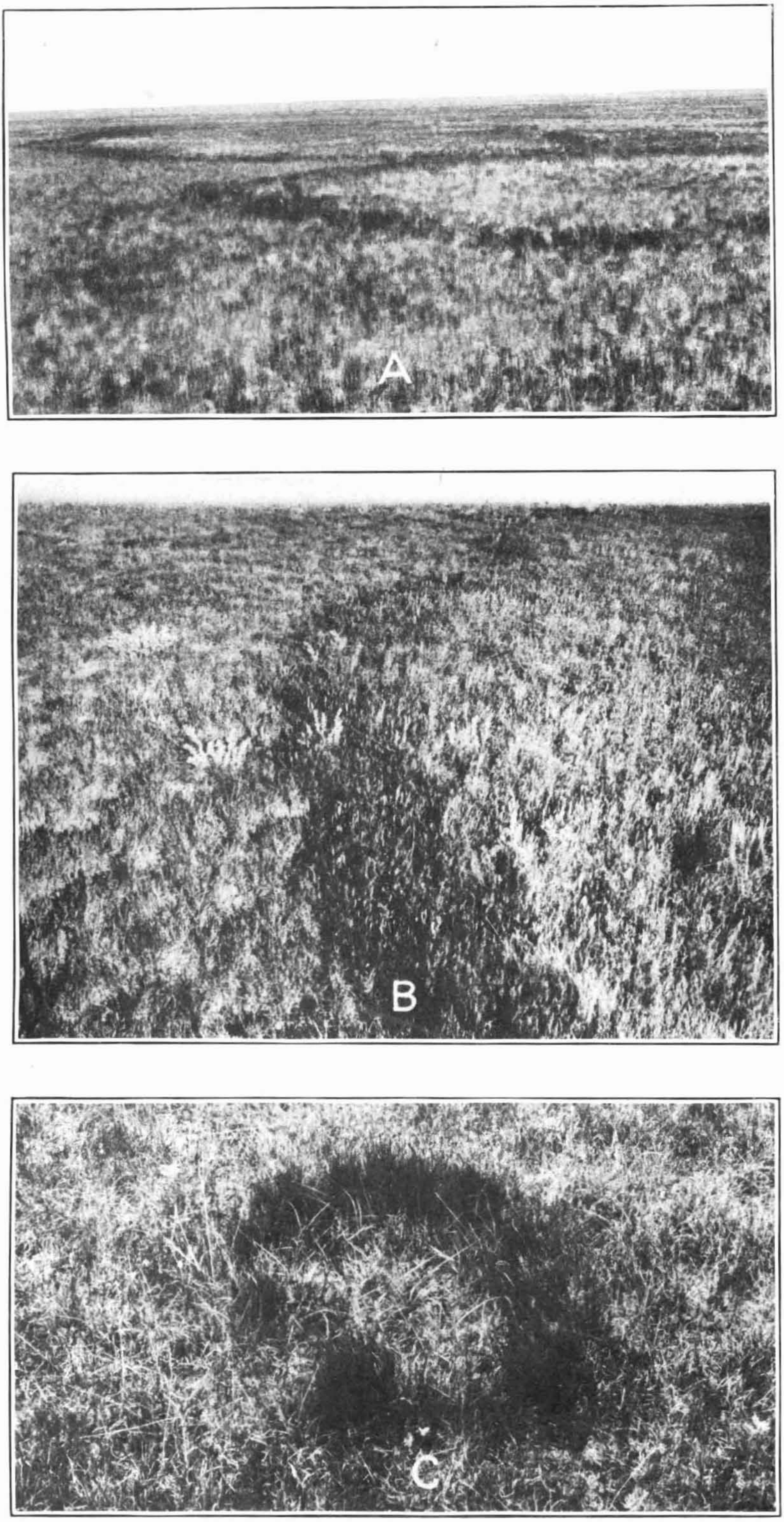
C.—A large fruiting body 30 cm. across, which for some reason has split open during the early growth period. The dry air has cured the tissue before mature spores were formed. Fruiting bodies of this fungus are often found in this condition. Akron, Colo., July 7, 1909.

PLATE 30

A.—The effect of a ring of *Agaricus tabularis* on the native vegetation. In this ring the short grass is dying or dead, but *Gutierrezia sarothrae* is a little larger and much greener in color than either outside or inside the ring. Akron, Colo., July 25, 1909.

B.—A ring of *Catastoma subterraneum*. The only outward evidence of the presence of this fungus is the stimulated growth of *Plantago purshii* and the slightly deeper green of the short grasses. The mycelium is not easily distinguished in the soil, although the fruiting bodies are just breaking through the soil. Akron, Colo., August 16, 1915.

C.—A very small ring apparently caused by a fungus but marked only by a more luxuriant growth of *Festuca octoflora*. Akron, Colo., June 15, 1915.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